The American Midland Naturalist

Devoted to Natural History,

Primarily that of the Prairie States

FOUNDED BY J. A. NIEUWLAND, C.S.C.

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THE PHYLOGENY OF ZEA MAYS*

PAUL WEATHERWAX

FOREWORD

So much has been said and written about the phylogeny of the maize plant that the offer of any new general treatment of the subject may require a word of justification. Various approaches to the problem in the past few years have, however, yielded a considerable accumulation of new information of value. The natural geographic range and botanical nature of teosinte are now much better known than they were a short time ago; new methods of dissection of the pistillate inflorescence of maize have made it possible to correlate it almost exactly with the inflorescence of some other grasses not previously considered in connection with it; and a study of the development of certain anomalous structures suggests an explanation of the ear of corn in terms of spiral phyllotaxy. A review of evidences previously considered is naturally a prerequisite to the proper utilization of this new material.

Assistance received from various sources in the pursuit of this problem is gratefully acknowledged. Grants from the National Research Council, the American Association for the Advancement of Science, and the Society of the Sigma Xi made possible a visit to the highlands of Guatemala in 1932, where a study was made of the physiography and grass flora of a portion of what is thought to be the homeland of maize. This work was also made much easier by the fine support given me in all possible ways by representatives of the United Fruit Company. Financial support for this study, as well as the more comprehensive one on the morphology and phylogeny of the grass family, has been provided for several years by the Waterman Foundation of Indiana University.

* Contribution No. 66 from the Waterman Institute, Indiana University.

Introduction

A combination of many circumstances gives to the origin and natural relationships of the Indian corn plant an unusual interest. We are often niggardly in our strictly botanical attention to plants best known for their usefulness; but the striking aspect, high specialization, and great variability of this plant have made it an object of extensive scientific studies, many of which have had no immediate utilitarian objective. Most of these investigations sooner or later project themselves into the past, and there we find the history of the ancient American races of men no more mysterious than is the record of the plant which was the economic basis of their cultural attainment.

To find among wild plants, living or extinct, the prototype of a domesticated form is a peculiar problem, and it usually offers more difficulty than would be expected. The improvement of a wild plant through domestication is at best a slow process which involves so little of the spectacular that it is not likely to be recorded in detail; the human part of the process may, in fact, be done unconsciously, and its significance may be realized only long after the fundamental parts of it have been accomplished and its beginnings have been forgotten. If, as is evident in the domestication of maize, the process began long ago, and through the agency of a people taking only its first step toward civilization, the difficulty of finding out anything about it by direct methods is greatly increased.

European civilization made its first effective contact with maize only a little more than four centuries ago. For our purpose it matters little whether or not the early Scandinavian visitors to America saw maize;[1] even if they did, they did not know the significance of their discovery and did not take the plant to Europe. Accounts of indefinite date or uncertain value in the literatures of Europe and Asia have been interpreted as references to maize, and it is possible that the plant may have been taken to the eastern hemisphere before the discovery of America by Columbus;[2] but, if such thing did happen, no lasting effect came of it.

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1 Fernald (1910); Andrews (1913).

2 The evidences on both sides of this question have been summarized by DeCandolle (1884, pp. 387-393) and by Collins (1909, pp. 20-25).

The similarities which have been observed or imagined between the eastern systems of writing and those of the Aztecs and Mayas, and the alleged portrayal in ancient American art of objects known only in the Old World, may be regarded as evidences of a recent connection between the peoples of the two hemispheres; but the evidences from agriculture indicate a separation ante-dating civilization. It has been pointed out that not a single important cultivated plant, and no domesticated animal except the dog, was common to the two systems of cultures.[3]

Our first dependable accounts of the maize plant by the Spanish explorers of Mexico and Peru and by the first English colonists in Virginia and Massachusetts indicate that it was then essentially the same highly specialized plant that it is today. It was then, as now, completely dependent upon man for its continued existence, and the search for its ancestry became a living problem.

The information that has accumulated since then has come from many sources: from Indian myths and legends, from the work of the archeologist, from the accounts of explorers, from paleontology, and from the botanical nature of the plant itself. The evaluation of each bit of evidence has necessarily taken into full consideration the nature of its source. The meagerness of the direct evidences contributed by historical sources emphasizes the value of those coming from a study of the plant and its near relatives. When taken all together the fragments of information that we have do not fit together into a picture which all will accept as expressing a fact. We have had, rather, a series of growing theories, necessarily recast from time to time in the light of new discoveries or new interpretations.

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3 Merrill (1930, 1933).

Archeology and Exploration

The most satisfactory picture of the prototype of maize would be one furnished by the historian. That is, if we could find in manuscripts or inscriptions left by the aborigines, in rational and literal traditions, or in the records of dependable observers of the early days of European exploitation of America any definite accounts of the occurrence of wild corn or of the process of domestication, such evidences would have very great weight. The antiquity of American agriculture, however, greatly diminishes our hope of definite information from these sources.

Indian Traditions.—Throughout the prehistoric range of the corn plant every race probably had a story of the origin of maize agriculture; but these stories had undergone such a process of conventionalization in oral transmission that if they had in the beginning any basis of reality, this had disappeared long before the coming of the white man. In each of these stories there is the same indefiniteness as to time, and usually as to place, and the same lack of reference to any material change made in the plant in the early days of its domestication. It is always some bird or animal which brings maize to a famishing hero, or some divine agency which gives seed of it to a chosen tribe and teaches them the rudiments of agriculture; and the maize plant received in each instance is the full-fledged, highly specialized plant that we know today. After working through the voluminous mass of legend of this kind, looking for scattered fragments of truth, we are forced to conclude that these stories have little basis of fact derived from observation but are comparatively recent products of a subjective inquiry into the past.

The only written documents of the native American races that have been preserved are a few manuscripts probably less than five hundred years old. One of these, the famous Popol Buj of the Quichés of northern Guatemala and southern Mexico, written by an Indian early in the sixteenth century, gives what is regarded by many as the oldest written account of the origin of maize culture.[4] It proves to be nothing more than a simple story of the introduction of the plant in its modern form from a nearby region.

Archeological Discoveries.—In the past few years there has been an increased interest in a type of archeological work which promises an important contribution toward the solution of our problem. The ruins of the old Aztec and Inca empires were brought to the attention of the public long ago, but, as commercial explorers have made their way into the tropical jungles, and as the accomplishments of scientific workers have been popularized, we have begun to realize that the region between Tehauntepec and Panama holds the record of one of the greatest of the native American civilizations.

The ordinary reader, however, in his occasional contact with the names of Uxmal, Quiriguá, or Chichen Itzá, has little conception of the wealth of

4 Villacorta & Rodas (1927, pp. 297-299). For an English translation of a part of this account see Sturtevant (1919).

material that is still to be utilized in developing the picture of the Mayan people. The map of southern Mexico and Guatemala is already dotted with the sites of unexplored ruins, and the traveler over railroad or mule trail is never long out of sight of some vestige of this vanished civilization.

A part of the message carried by these ruins certainly pertains to maize, for it has been used as a pattern for design in pottery and in ornaments, and some symbols in the picture writing evidently refer to the deities of maize and of agriculture. But the destructive work of religious fanatics in the days of the conquest largely broke the connecting link between us and the past, and the whole mass of written record still awaits its Rosetta Stone.

Although these records will later tell us much about the lives of the people who left them, we must not hope for too much about the origin of the maize plant. They will give us hardly more than a check on the accuracy with which the traditions of the race have been transmitted to us in recent times. Like the traditions extant at the time of the early explorations, these ruins belong to a time so far removed from the event in which we are interested that the people who left them had no significanct advantage over us as to position in the lapse of time.

Reports of Wild Maize.—Granting that the ancient Indian did develop the cultivated plant from some wild species which continued to grow spontaneously in its natural habitat, there is a bare possibility that his descendants today might recognize the similarity; or the wild plant might have been found by some explorer since the cultivated plant was brought to the attention of European civilization.

In this respect the Indian is of little help to us. In parts of Mexico, teosinte[5] or hybrids of maize and teosinte were sometimes mentioned as the source of cultivated corn,[6] and the Iroquois of New York applied to pod corn a name which signified "original corn."[7] Other records of the same kind are found, but it is doubtful whether they represent anything more than a whimsical idea of the Indian farmer. Ordinarily the Indian's philosophy did not require a prototype for maize. It came to him in its present form from some other race of Indians or through some supernatural agency which defied explanation.

The European, coming as an explorer or an immigrant, was more rational. He knew in many cases the connection between his cultivated plants and their wild ancestors, and he assumed a similar relationship for maize. Travelers and explorers have, accordingly, made occasional mention of wild maize or given tantalizing pictures of plants which might have furnished clues; but

5 *Euchlaena mexicana.* This peculiar Mexican forage plant will be described in more detail later; see page 20. According to Kroeber (1923, p. 353) the common name is derived from the Aztec *teocentli*, which means "divine maize." The correct pronunciation is te-o-sin'-te. It is probably to preserve the final syllable in pronunciation that other spellings, such as *teosinté* or *teosinthe*, are sometimes employed.

6 Watson (1891, p. 160).

7 Parker (1910, p. 43).

much of this testimony is invalidated by the observer's lack of the technical knowledge necessary to evaluate, or even to report accurately, what he saw.

Wild Corn in Mexico.—One of the earliest of these reports was published in 1746 by Boturini, an Italian, who had a few years previously engaged in extensive explorations and historical studies in Mexico. He says that he found wild maize growing in the forests of the warm country. He describes the ears as small and speaks of the excellent flavor of the grains. A native tradition for which he is the authority says that the ancient Indians first learned the food value of maize by tasting the roasted grains which they found in burned-over forest areas and then began to cultivate corn by planting grains which had not been damaged by the fire.[8]

Collins (1931) pertinently questions whether the plant really grew wild and whether it really was maize. He thinks it improbable that any plant able to survive under the conditions indicated would be enough like modern maize to be called maize.

Accounts from Paraguay.—Two reports from Paraguay indicate that pod corn, a variety which has husks enclosing each individual grain, and which is regarded by many investigators as embodying primitive characteristics, was once cultivated there. Both Azara (1809) and Saint-Hilaire (1829) state that pod corn was included among the varieties grown by the Gauycuru Indians. Collins has reviewed these two reports and says that references to the second have, without apparent warrant, assumed that pod corn grew wild in Paraguay.[9] He also quotes from Azara a description of what the latter regards as a variety of corn in which the grains are borne in a terminal panicle. When this cluster of ripe grains is boiled in oil the grains pop but remain attached to the framework of the inflorescence.[10] These reports are certainly interesting, and further information, particularly on the last, would be welcome; but we cannot at present definitely connect them with wild maize.

Teosinte as Wild Maize.—The close resemblance between maize and teosinte immediately suggests a near relationship, and many attempts have been made to establish the fact that the Indian developed the former from the latter by some sort of selection. This theory will be discussed fully later; it is sufficient to say here that, almost without exception, it is rejected by those who are familiar with the morphology of both plants.

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8 Mrs. Nuttall, to whom we are indebted for the discovery of this story in Boturini's work, and whose abstract of it (1930) is my authority for its content, regards this as a very reliable account and thinks the wild plant may yet be found somewhere in Mexico. Schellhas (1929) also regards this as a possible solution of the problem.

9 Collins (1919a). DeCandolle (1884, p. 394) also notes that there is in the original statement no evidence that plant grew wild.

10 This might not have been a variety of corn at all. Cook (1925, p. 36, f. 3) mentions a Peruvian species of Amaranthus whose seeds pop like pop corn. Azara is indefinite in his description and may easily have been so far influenced by the food value of the plant as to have overlooked its natural affinities. It must be remembered, too, that those who do not have the botanical view point are sometimes inexact in the use of such words as *corn* or its equivalent in other languages. Even we regularly call a member of the Polygonaceae a kind of wheat (buckwheat) and allow it to become associated with the true cereals in our agricultural statistics.

Much more deceptive have been the natural hybrids between maize and teosinte frequently encountered where the two plants grow near each other. Anyone discovering one of these hybrids in an area not at the time under cultivation, and not knowing of the cross-fertility of the two species, would be justified in at least the guess that he had found wild maize. Watson was thus deceived and described a hybrid as a new species, and Harshberger amplified the error by making the hybrid the basis of an extensive botanical study, assuming it was wild maize.[11]

A Recent Report from Guatemala.—The most recent report of a plant thought to be wild maize is given by Mrs. Nuttall in her account of Boturini's statement. She quotes[12] a part of a letter from Oliver La Farge, who has done extensive ethnological work in the highlands of northern Guatemala. The letter says that at Finca Chanquejelvé, near Nentón, there is a wild plant whose small "ears" are used for food and have the flavor of maize.

While in Guatemala, in the spring of 1932, I made an effort to learn more about this plant. Circumstances made it impossible for me to visit the exact locality where the plant grows, but I found Mr. La Farge at Huehuetenango and secured from him further information. He did not see the plant in question but encountered the whole "ears" of it once as a constituent of a soup. He describes them as being two to four inches long and made up of small objects like grains of corn arranged in four longitudinal rows equally spaced around an axis. The silks (styles) which would be expected on corn were lacking. The flavor suggested that of green corn. Nothing was learned of the nature of the plant as a whole except that it grew wild.

This is an interesting report, but some questions will still have to be answered before it can be accepted as conclusive evidence of wild maize. It would be unusual for the whole "ears" of any maize-like plant to be used for food at the stage of development indicated, that is, when the grains were large enough to taste like corn. Long before this the axis would have become so woody as to make it unfit for food. The pistillate inflorescence might be used for food, as those of other plants sometimes are, but in that case we should have to explain the absence of the styles. The equal spacing of the rows of grains would be unusual unless the plant at this stage lacked one very important maize characteristic, namely, the full development of a grain in each spikelet of the normal pair.[13] The flavor of corn would ordinarily be regarded as significant and not easily mistaken by anyone familiar with the plant; but in the heterogeneous collection of vegetables and aromatic herbs that enter into the preparation of soups by the native cooks of the country no ordinary mildly flavored vegetable like corn would have a chance to assert itself sufficiently to be identified.

After a discussion of the various aspects of the problem with Mr. La Farge

11 Watson (1891); Harshberger (1893).

12 Nuttall (1930, footnote, p. 219).

13 See page 31.

we concurred in the opinion that, without further corroboration, we should not feel justified in assuming that the plant was in any way closely connected with maize. It might as well have been the inflorescence of any one of several species available in the vicinity at that time of the year (early May) and frequently used for food. The locality is, however, theoretically right for wild maize, and an effort is being made to secure more information concerning this report.

Geology

Of all the records that we have of life in the far-away past the paleontological is the most reliable. Even a definite statement left by a human observer may be so influenced by his limitations or by his interpretations as to be practically useless; but the record left in the rocks, exact, unchanged, and dated, may be read again and again and reinterpreted in the light of broader understandings and new abilities of science. Its one great defect is its fragmentary nature, and in the case of maize it is thus far almost a blank.

By a sufficiently broad application of the word *fossil* it may be said that a few fossil remains of the corn plant have been found. The geological term is deceptive, however, with its promise of antiquity, and the remains of the plant falling into this class add no significant detail to our picture of its earlier character.

Darwin's Report.—Reference has frequently been made to Darwin's discovery of fossilized remains of maize, along with marine shells, bits of cotton thread, and plaited rush in a deposit, then eighty-five feet above sea level, on the island of San Lorenzo, off the coast of Peru.[14] The facts ordinarily stated in these references might easily lead to the inference that the fossil was in a marine deposit, and Darwin says that he himself at first thought so. On further examination, however, aided by a correlation with formations on the mainland, he concluded that at some remote time when this surface was lower, but still well above sea level, some violent earthquake had caused the sea to break over the beach and leave a deposit of mud and shells.

Inasmuch as human relics were present in the formation, the marine shells would not necessarily indicate an inundation by the sea, particularly if they happened to be the shells of species which the Indians might have used for food. The immense mounds of shells which they have left in other places, near long-used camp sites, are frequently mistaken for natural deposits. This possibility removes the necessity of assuming any great change in the elevation of the deposit after its formation and takes away much of the presumption of extreme age; and this conclusion is substantiated by the fact that the cotton threads and the rushes were still in good enough state of preservation to be identified.

A Fossil from Peru.—Another fossil, described by Knowlton (1919), consists apparently of an ear of corn whose tissues have been completely replaced by minerals. It was procured from a dealer in curios at Cuzco, Peru, and

14 Darwin (1930, pp. 380-381).

nothing is known as to its origin or age or the conditions under which it was preserved. Both Knowlton and Collins (1919b, 1923), who later discussed the specimen, indicate that it has no character essentially different from those of varieties of corn grown in Peru today.

Collins cites this as "the first tangible evidence of the geological existence" of the plant, and says further that "the origin of maize may now be transferred from prehistoric to geologic times, for Dr. Knowlton is confident that, although the specimen may not be assigned to its exact geological period, it is an undoubted fossil."[15]

What bearing this transfer from "prehistoric" to "geologic" time has on the origin of maize is not clear, inasmuch as geology rightly lays claim to all time, including the present. If, however, the utilization of geologic terminology means to imply that the specimen under consideration is of extreme age, the argument may well be questioned.

Without knowing more definitely what type of fossilization is represented in the specimen it would be futile to speculate about the time that would be required for the process, and, indeed, the general works on fossil botany avoid definite statements as to the probable time needed for various types of petrifaction. Seward (1898, p. 92) and Solms-Laubach (1891, pp. 28-33) indicate that silicification may make perceptible progress in less than a century. Knowlton's fossil retains no organic structures in the grains or the cob, the only differentiation being in color. The specimen may be only a cast made by natural methods in a mould left by the decay and removal of an ear which had been buried; and it seems that this type of replacement may equally well have been accomplished in a comparatively short time,—even well within the period of recorded history.[16]

"Petrified Corn" in Georgia.—A number of reports of fossilized parts of the maize plant have been brought to my attention in the past several years, but none have yielded any results of value. One of these, however, has had such wide publicity that an account of it is in order. Some years ago a student in the University of Georgia told me that a lady living in the southern part of that state had a fossil ear of corn which had been found near her home. Inquiry brought from many sources the information that it was undoubtedly a "petrified" ear of corn, that it indicated the origin of corn in Georgia, that renowned scientists had expressed great interest in it, and that fabulous prices had been offered for it. When definiteness was demanded these stories suffered considerable shrinkage and were finally reduced to the owner's own account. There proved to be several of the specimens, and they had been picked up in a field where corn had been fed to hogs fifty years be-

15 Collins (1919b, p. 170).

16 Since the above was written it has been rather conclusively demonstrated that this supposed fossil is an artifact. It seems to be a rattle, made of clay and partially baked, its only connection with maize being that an ear of the latter was copied by the artisan. See: Brown, R. W. The supposed fossil ear of maize from Cuzco, Peru. Journ. Washington Acad. Sci. **24**: 193-196. 1934.

fore. The local hypothesis was that ears which had been trodden into the mud had become fossilized.

Only a superficial examination was necessary to show that the corn plant was in no way responsible for the formation of these specimens. Each is a cluster of hexagonal crystals arranged around an elongated axis, the whole resembling homewhat an ear of corn (Fig. 1). Some which are split or broken transversely show a reddish or brownish central region which has just enough resemblance to a cob to be deceptive. They range in diameter from an inch to something like four inches, and large pieces of the same mineral, weighing fifteen or twenty pounds, were pointed out as having come from the same locality. Not even in a museum could such a range in sizes of ears of corn be

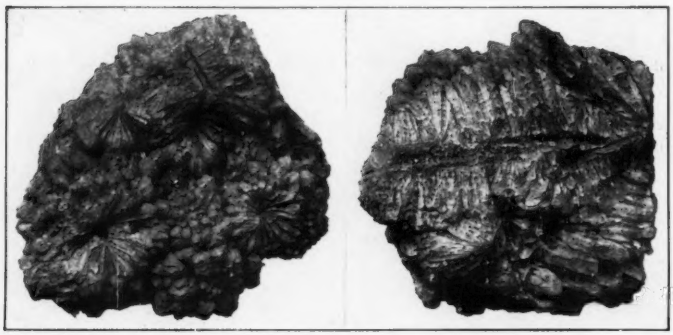

Fig. 1. A crystalline mineral from southern Georgia, which has erroneously been regarded as a fossil of maize.

found, and it is evident that no such heterogenous variety of corn ever grew there. Many of the crystals, supposed to be petrified grains, are larger by far than any grain of corn that has ever been known, and their shape and arrangement further contradict any theory that they are in any way connected with the corn plant.

This report adds nothing to our knowledge of maize, but it has been responsible for such widespread misinformation that a refutation of what it implies should be on record.

Value of the Fossil Record.—The few authentic remains of the plant that may be called fossils differ in no significant way from fragments that have been found in tombs, in the ashes of ancient fireplaces, and among other relics of the prehistoric races. It would be difficult, indeed, to draw any sharp line between fossils and archeological specimens, and there is no good evidence that the specimens cited as fossils are very old. If we abandon the idea that the formation in which Darwin's specimen was found has undergone considerable elevation, everything else indicates that it is recent; and the history and nature of Knowlton's specimen are too obscure to permit it any great value.

There is a strong presumption that both specimens fall within the past four or five thousand years at most.

The barrenness of the geological record should not cause surprise; it is rather to be expected. If a plant is to leave its signature in the rocks, it must have structures which are capable of being fossilized, and these must become covered by the preserving medium before they have had time to decay or be destroyed in other ways.

The maize plant meets the first requirement fairly well; but it falls short of the second. Its stems, ears, grains, and cobs are firm enough to leave their marks in a formation, if they should be quickly and effectively covered. But the plant has probably been a mesophyte at least since its origin as a separate species, and practically its only chance of reaching a place where it could make geologic history has been when man placed it there. That was, of course, long after the period in which we are primarily interested.

Taxonomic Position

Having obtained little information from these more or less direct sources, we turn next to the living maize plant itself, to find in it, if possible, some vestigial reminders of the past; and we test and amplify our findings there by comparing maize with certain other plants which have evidently shared a part of its history. This becomes peculiarly a botanical problem, to be solved by methods which the botanist has devised for reconstructing the past. Our result can be at best only a theory, an imaginary picture of a plant which once lived, but no actual remnant of which is known today. This picture must utilize as much as possible of what we know of the modern plant and its near relatives, and it must be consistent with all that we know about them.

Classification of the Grasses.—The grass family,[17] to which maize belongs, is a very clearly defined group of plants, but it comprises such a large and varied aggregation of forms that it has been divided into a number of tribes. Different authorities disagree as to the position of many genera, and somewhat as to the limits of some of the tribes, but the following classification is probably a fair compromise:

GRAMINEAE — THE GRASS FAMILY

1. *Bambuseae:* the bamboos.
2. *Phareae:* several tropical genera, *Pharus, Olyra, Lithachne,* etc.
3. *Festuceae:* the fescues, bluegrasses, brome grasses, etc.
4. *Aveneae:* the oats and their relatives.
5. *Chlorideae: Chloris, Bouteloua, Leptochloa, Eleusine, Cynodon, Spartina,* etc.
6. *Hordeae:* wheat, rye, barley, etc.
7. *Agrostideae: Agrostis, Sporobolus, Muhlenbergia, Aristida, Stipa, Phleum, Alopecurus,* etc.
8. *Zoysieae (Nazieae): Anthephora, Hilaria, Osterdamia,* etc.

17 *Gramineae,* or *Poaceae* in recent literature.

9. *Phalarideae: Phalaris, Hierochloë, Anthoxanthum,* etc.
10. *Melinideae: Melinis, Arundinella.*
11. *Oryzeae:* the rice tribe.
12. *Zizanieae:* the wild rice of North America and a few other genera.
13. *Paniceae: Panicum, Paspalum, Cenchrus, Setaria,* and a large number of mostly small, tropical genera.
14. *Andropogoneae:* a large tribe, sub-divided as follows:
    a. *Sacchareae:* sugar cane, *Eulalia,* etc.
    b. *Euandropogoneae: Andropogon,* the sorghums, etc.
    c. *Rottboellieae: Elyonurus, Rottboellia, Hackelochloa,* etc.
15. *Maydeae (Tripsaceae):* divided geographically as follows:
    a. Oriental genera: *Coix, Sclerachne, Polytoca, Chionachne,* and *Trilobachne.*
    b. American genera: *Tripsacum, Euchlaena, Zea.*

The Maydeae.—The tribe *Maydeae*[18] is characterized in general by the highest degree of specialization that has been reached in the grass family. In all recent classifications it has consistently included the genera indicated, with the exception of *Trilobachne,* which has only recently been separated from the somewhat overlapping *Polytoca* and *Chionachne.*[19] Some authorities have also placed here the peculiar Brazilian genus, *Pariana,* but it apparently has little in common with members of this tribe.

Coix, Sclerachne, Polytoca, Chionachne, and *Trilobachne* are all native of the region extending from India and Burma through the East Indies and into Australia. The general character of members of this group is shown in Figures 2 and 3. Some species have a wide range in this region, but others are limited to very small areas. *Coix,* the best known of the group, is now widely distributed, in a large number of intergrading and interbreeding forms in all the warmer parts of the world. Some varieties are grown as cereals; the round, hard-shelled fruits of others are used for beads and have been responsible for the common name of the plant, Job's tears. The other genera are made up of a number of closely related species which have been treated in variuos ways by taxonomists.[20]

The other three genera are American. *Zea,* represented by a single species, *Zea Mays,*[21] which includes all varieties of maize, is known only in cultivation. At the end of the fifteenth century it was the basis of practically all agriculture in America from the latitude of the Great Lakes to northern Argentina and central Chile. *Tripsacum* (Fig. 4, A-C) is represented by *T.*

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18 *Tripsaceae* in recent literature, in conformity with the type code of nomenclature. It is in accord with the same code that *Poaceae* has been substituted for *Gramineae* as the name of the grass family. The older names, however, are still widely used and are certainly more intelligible to the general reader at present.

19 Henrard (1931).

20 Henrard's classification (1931) gives the synonymy.

21 For an explanation of this name and a discussion of the subdivisions of this species see pp. 55.

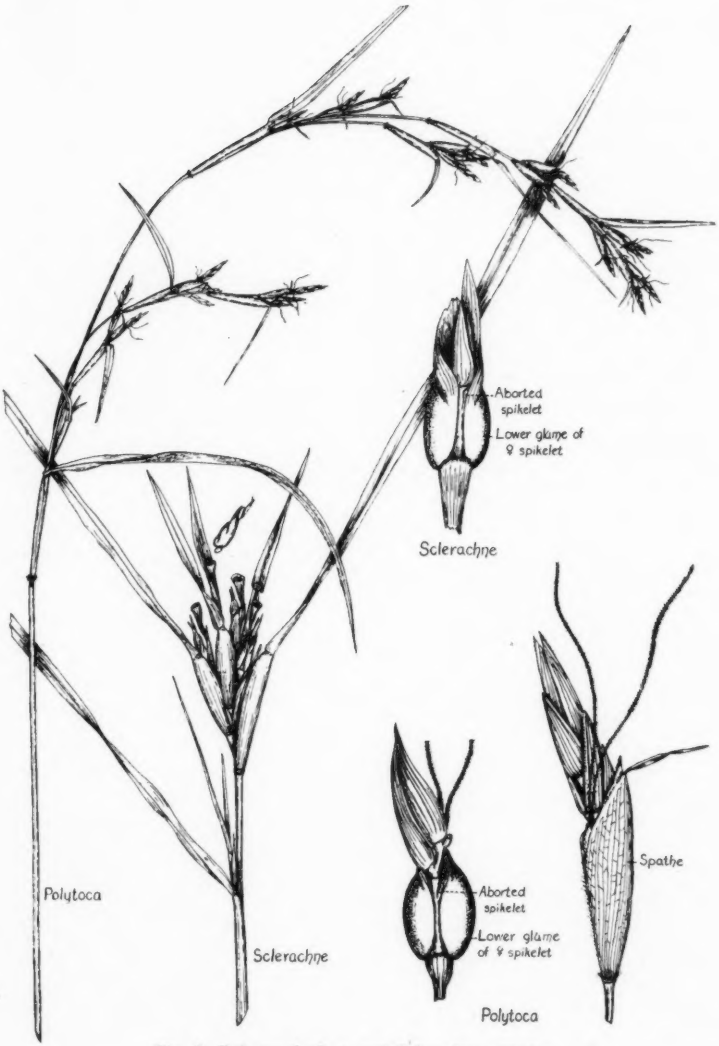

Fig. 2. *Polytoca barbata* and *Sclerachne punctata*.

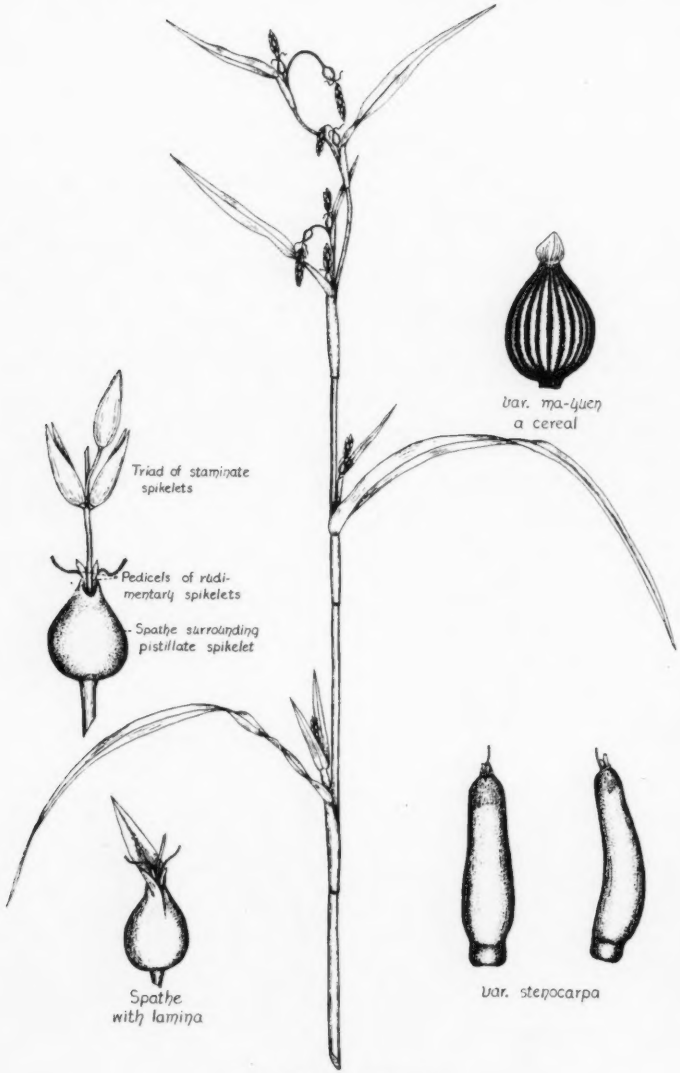

Fig. 3. *Coix lacryma-jobi.*

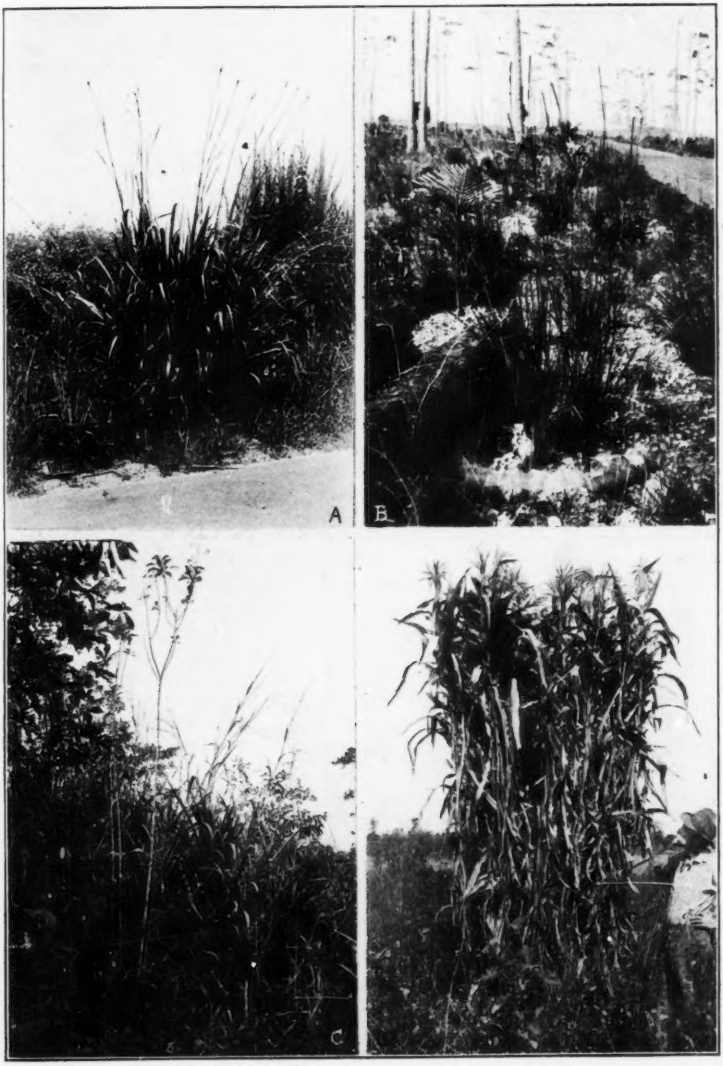

Fig. 4. *Tripsacum and Euchlaena.* A, *T. dactyloides* (Okeechobee, Florida); B, *T. floridanum* (Homestead, Florida); C, *T. latifolium* (Quirigua, Guatemala); D, *E. mexicana* (cultivated in Florida).

dactyloides from the southern part of the United States to Brazil, and by a number of other species less widely distributed within the same general range. It has some value as a forage plant today but was probably of no economic value to the Indians.

It is generally conceded that *Euchlaena,* commonly known as teosinte, is the nearest living relative of maize. There are two clearly defined species, *E. mexicana* and *E. perennis.* The latter has a limited distribution in southern Mexico.[22] *Euchlaena mexicana* (Fig. 4, D), which is an annual, has a natural distribution, chiefly as a weed in cultivated fields or other protected places, in the plateau region of central and southern Mexico and in Guatemala. Its range has probably been much the same since prehistoric times, and there is no indication that it was cultivated or that it was used to any great extent by the aboriginal races. It was introduced on a few seed farms in Florida several years ago, and near Lake Apopka it seems to be persisting as an escape.

The geographical separation of the *Maydeae* into two parts, one in the Eastern Hemisphere and the other in America, makes it seem very unlikely that the two groups have recently been united, and morphological characters give further evidence of a wide phylogenetic separation.[23] Almost no one in recent years has seriously considered the Malaysian group as very near relatives of maize, and it is my opinion that they can safely be disregarded in considering its ancestry.

Characteristics of the Maydeae.—The *Maydeae* are distinguished from the other tribes of grasses by two characteristics: the spikelets are grouped in twos or threes on the branches of the inflorescence, and the flowers are unisexual. The first of these characteristics is present also throughout the great tribe *Andropogoneae,* and the second occurs in numerous species and genera scattered through most of the other tribes. There is no very good reason why monoecism or dioecism should be made the sole basis for forming a separate tribe, and this is not done in the case of *Cortaderia, Distichlis,* one or more species of *Poa,* a species of *Eragrostis, Buchloë, Jouvea,* etc., which are dioecious members of other tribes.

As a matter of fact, if we were to ignore monoecism as a significant phylogenetic character, throw the *Maydeae* back into the *Andropogoneae,* and adopt a new criterion of relationship, placing the main emphasis upon certain lines of evolution that have evidently been followed in the history of the paired spikelets, we could probably separate out of the whole a number of tribes which would recognize the community of origin of some genera now placed in separate tribes. In other words, some members of the *Maydeae* are probably much more closely related to some of the *Andropogoneae* than they are to some other members of the *Maydeae.*

In the *Andropogoneae* there are certain genera constituting a natural group which Hackel[24] recognized under the tribe *Rottboellieae,* which are so much

22 Hitchcock (1922); Collins (1921).
23 Weatherwax (1926).
24 Hackel (1890, pp. 45-52).

like some species of *Tripsacum* that they are undoubtedly closely related. A more detailed study of the American genera of *Rottboellieae* and *Maydeae* will afford a basis for a theoretical phylogeny.

Vegetative Anatomy

To anyone who sees in a superficial way the great range of variation in maize it must present a bewildering array of characteristics. The varying height of the plant, the number and size of its parts, its different kinds of inflorescences, the number and form of its branches, and the endless series of combinations of size , shape, color, and chemical composition of its grains

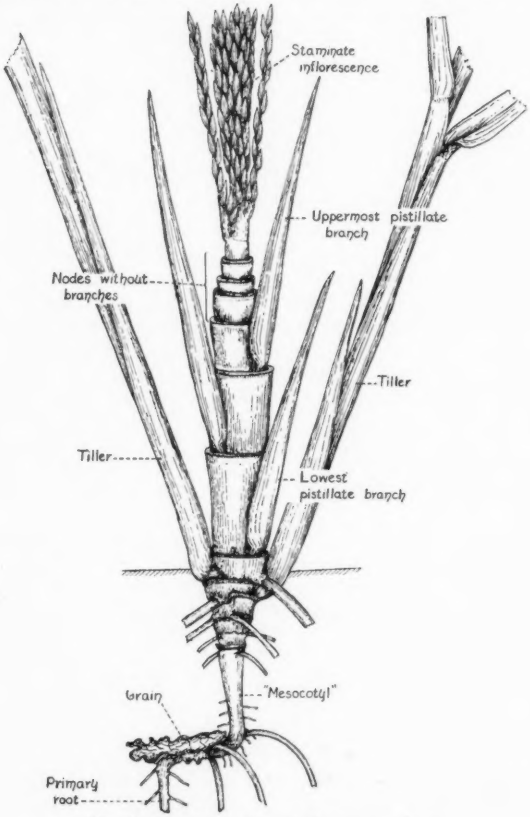

Fig. 5. Structural plan of the maize plant.

would seem to defy any attempt at generalized description. Limiting ourselves, however, to those features which are thought to afford dependable indications of past conditions, we eliminate much of the detail and find a gratifying uniformity in most of the otherwise diverse varieties.

System of Branching.— The plant consists of a dominant primary axis terminating in a staminate inflorescence and bearing below this two classes of primary branches (Fig. 5). One group of the latter is represented by one or more branches near the middle of the stem which bear the pistillate flowers and untimately the fruit. The internodes of these are so short that the leaf sheaths completely enclose the inflorescence until anthesis, and even then only the styles are exserted. Frequently the greater part of the entire branch remains inside the subtending leaf sheath of the primary axis until well after flowering. The primary branches of the other category arise from the lower nodes of the plant, which are usually underground. Some of these, which remain short and bear ordinary pistillate inflorescences, may be regarded as normal ear-bearing branches placed low on the plant. Others develop root systems of their own and become more or less independent, in which case they become replicas of the primary shoot. Between these extremes there are basal branches, probably dependent only in part on the main culm, whose inflorescences consist of both staminate and pistillate spikelets arranged in various ways.

Latent Buds.—As a rule, every leaf axil which does not have a branch has a bud of some kind. Below the ear, on the main culm, these buds are usually prominent, and in some varieties there may be a graded series from the main pistillate branch down through the smaller structures of the same kind to buds which have no function. Above the ear these buds present more of a problem inasmuch as they are not always easily detected. Definite evidences of their existence in such cases are seen, however, in the flattened side of the culm and the active embryonic region in the position in which they would be expected. In some less specialized varieties, moreover, functional pistillate branches may appear in all the upper axils except possibly the topmost one. In the axils of the sheaths covering the pistillate inflorescence the buds are usually prominent and frequently develop into functional pistillate shoots.

Annual Habit.—All forms of maize are annual. Some varieties are said to require more than a year for the complete life cycle, but in these the plant goes through a definite series of steps of development and dies of old age as its seeds reach maturity. No variety shows any tendency toward the production of a rhizome or other underground modification which might extend the life of the individual beyond its first reproductive cycle. Although the basal offshoots are morphologically like those which in many other species enable the individual to live indefinitely, in maize these die with the rest of the plant.

Teosinte.—In the teosinte plant (Fig. 6) the primary axis plays a minor part, the various categories of branches forming the greater part of the adult structure. The basal branches of the primary axis may branch again and again from their lower nodes, finally producing, under favorable conditions, more than a hundred culms, which are indistinguishable from the primary one

Fig. 6. *Euchlaena mexicana* (from seed collected near Jutiapa, Guatemala).

except on very close examination. The main aerial branches differ from those of maize in having longer internodes and a vegetative structure generally similar to that of the basal branches. There is a tendency for branches of any order to continue branching from most of their nodes, and in vigorous specimens the result is a complicated system of branches of different orders.

Potentially at least, each culm, regardless of its order, terminates in an inflorescence. The main culm, the basal branches, and the larger aerial branches regularly end in staminate panicles resembling somewhat the corresponding structures in maize. On shorter branches, occupying lower positions on the plant, the inflorescences tend to be pistillate and are usually enclosed in the subtending sheaths with only the styles exserted. Many inflorescences have both staminate and pistillate spikelets, and a degree of hermaphroditism seems to be possible in almost any of them.

The species of teosinte *(Euchlaena mexicana)* commonly encountered in Mexico and Central America, and sometimes grown elsewhere for forage, is an annual with a slight tendency toward the perennial habit through the persistence of basal offshoots or of fallen culms, which develop roots at their nodes. Another species *(E. perennis)* has in its aerial parts much the same appearance but develops an extensive system of rhizomes, by means of which the individual lives indefinitely.

Tripsacum.—The several species of *Tripsacum* vary widely in the size and general aspect of the individual, but there is no doubt as to the close phylogenetic unity of the genus. All the species are perennial by means of rhizomes. The aerial stems branch, often repeatedly, and each branch ordinarily ends in an inflorescence composed of one or more spike-like structures bearing pistillate spikelets below and staminate above. The most widespread species, *T. dactyloides* (Fig. 7), embodies the significant characteristics of the species.

The Rottboellieae.[25]—The similarity between *Tripsacum* and some members of the sub-tribe *Rottboellieae* is so striking that it cannot be ignored as an evidence of close relationship; and from *Manisuris,* which is most like *Tripsacum,* a graded series can be traced through such genera as *Hackelochloa, Elyonurus,* etc. toward the more generalized types of the *Andropogoneae.* Some aspects of this series can be seen in Figure 8.

The only significant characteristic by which these genera can be separated from *Tripsacum* is that the latter is monoecious while the former have a part of their flowers perfect. It seems almost cretain that they and at least the American division of the *Maydeae* have arisen from the same branch of the Andropogonean stock and are more closely related to one another than to the main body of the *Andropogoneae.* The reconstruction of this branch of the family tree should follow a thorough study of geographic distribution and an investigation of certain lines of evolution which are evident from the present forms of inflorescence.

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25 Bentham & Hooker (1883, vol. 3, part 2, p. 1082); Hackel (1890, p. 52). Hackel excludes *Elyonurus* from the *Rottboellieae,* but largely on an artificial basis.

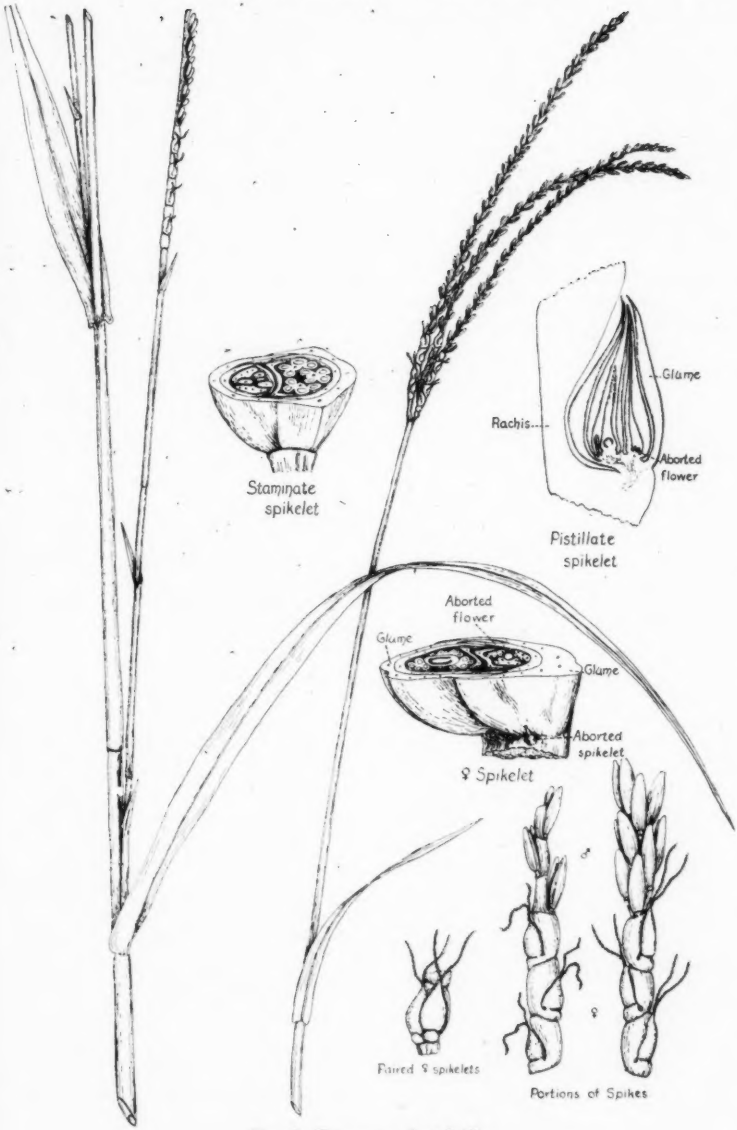

Fig. 7. *Tripsacum dactyloides.*

Ecological Evolution.—It is difficult to formulate any simple rule by which the seasonal behavior of a plant may be utilized in determining its past history, but there are many good indications that in the grass family the ecological evolution has proceeded generally from the moist tropical toward the drier, cooler habitats marked by wide seasonal variations.[26] This implies a tendency toward the annual habit and suggests that annual teosinte and maize have been evolved from perennial forms. Perennial teosinte naturally suggests the ancestor of the former, but no plant now known satisfies the requirements of the perennial ancestry of maize.

The rhizomes of all these perennials arise originally as basal branches of the main stem of the seedling, and subsequent aerial stems arise from them. The attainment of the annual habit has involved the suppression of the rhizomes, and all the aerial branches that would have arisen from them, and the strengthening of the primary axis and the encouragement of the aerial stems arising from its base. In the development of the typical grass plant from the seed there is a region in the lower part of the primary axis, usually underground, in which it is difficult to distinguish the nodes from one another except by means of the leaves. This makes it possible for a large number of branches to arise close together, and this condition is intensified by the fact that each branch has a similar region in its own lower part. In some perennial species the development of one or more rhizomes in this position may have an inhibiting influence on the production of aerial branches. Those species which abandon the production of rhizomes may thus fully express the potentiality for basal branching.

Annual teosinte seems to have done just this, and the extensive basal branching in some varieties of maize suggests a similar history for it; but in most highly bred varieties of the latter, basal branches almost never develop, and the extensive array of variously suppressed axillary buds constitute all that is left of a system of branches lost in phylogeny.

Artificial Influences.—The suppression of all kinds of branches to the end that the fruit of the plant is concentrated into a few units has made it more useful, and for the promotion of this line of evolution credit must be given to the selective influence consciously exerted by the aboriginal corn grower. The innate ability of the plant to respond to this method of improvement by producing a fruit abnormally large for the grass family is the principal characteristic separating maize from other grasses and adapting it to the type of agriculture practiced in America in ancient times.

A second inherent peculiarity which added to the usefulness of the plant was the shortening of most of the internodes of the pistillate branch. This enabled the leaf sheaths to form a protective covering over the inflorescence and fruit, an accomplishment of great agricultural significance but of doubtful or negative natural survival value.

Like the suppression of the branches, this invagination of the ear may have been influenced by artificial selection, but it seems highly improbable that it

26 Bews (1929, pp. 260-289).

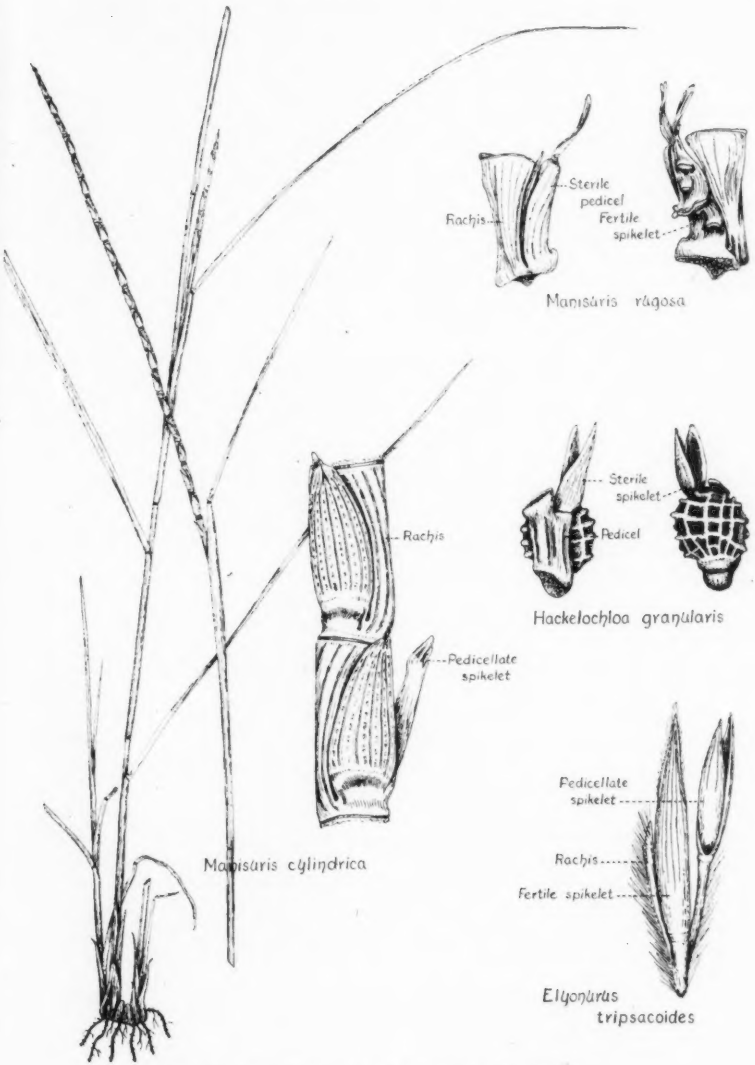

Fig. 8. Some members of the sub-tribe *Rottboellieae*.

was wholly due to this, for the same thing has occurred to a certain degree in several other grasses, and particularly in teosinte, which has never offered any reward for evolution in that direction. This step, moreover, is so closely connected with the increased size of the ear, due to the suppression of its own secondary branches, and with the reduction in the size of the bracts of the spikelet, that until it had been taken the plant probably offered little of economic interest to man.

Cytology and Genetic Compatability

A few of the genetic and cytological studies that have been made on maize have been extended to include closely related plants, but the total result proves disappointing when examined for evidences as to phylogeny. A part of this is due to the little consideration that has been given to the most significant members of the *Andropogoneae*, and a part of it to the limitations of the method.

Chromosome Numbers.—Cytological studies of maize have been made by many investigators, and the early differences of opinion as to the number of chromosomes are now fairly well reconciled.[27] The diploid number is typically 20, but variations from this up to 28 have been reported. Unequal distributions of chromosome numbers at the time of the reduction division sometimes result in haploid cells with fewer than the expected minimum of 10 chromosomes. These aberrant numbers, as well as unusual shapes and arrangements of chromosomes, are somewhat consistently characteristic of certain varieties or associated with definite genetic peculiarities.

The annual and perennial forms of teosinte have, respectively, 20 and 40 somatic chromosomes, and irregularities seem to be very infrequent.[28] In the species of *Tripsacum* which have been studied the prevailing diploid number of chromosomes seems to be 72, but one variety of *T. dactyloides* regularly has 36.[29] None of the published lists of chromosomes that have been available give any data on any of the *Rottboellieae*.

These chromosome numbers do not provide much basis for even a guess as to the course of evolution in this part of the grass family. The lack of any significant common factor which might be regarded as the basic number leaves only the hypothesis of change in individual chromosomes and the method of this is as uncertain as any other aspect of the evolution of the group. Even in teosinte the occurrence of twice as many chromosomes in the perennial species as in the annual offers something to think about if we are to assume that the annual form arose from the perennial. As Collins has indicated (1931) this case has an interesting parallel in the sorghums where *Holcus halepensis* L., which is perennial, has 40 chromosomes, while several closely related species have only 20, and one species has only 10.[30]

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27 Randolph (1928) summarizes the literature on chromosome numbers in maize.

28 Longley (1924).

29 Longley (1924) gives 35 as the haploid number for the material which he examined. In one count of 36 two of the chromosomes are regarded as univalents. Mangelsdorf & Reeves (41) give 18 and 36 as the haploid numbers of the two forms which they examined.

30 These figures are taken from the work of Longley (1932).

It may be that the determination of chromosome numbers in more species will enable us to interpret the data now at hand, but at present the story for these plants may be read as well in one direction as in the other, and it tells little in either.

Hybridization.—Aside from the similarity in general structure, one of the best evidences of close relationship among the American *Maydeae* is the ability of the different members to hybridize. The genetic incompatibility of two plants is not alone a proof of wide phylogenetic separation, for varieties which are undoubtedly closely related sometimes refuse to hybridize, and even perfect-flowered individuals are sometimes self-sterile. The converse of this proposition, however, carries more weight; and the production of hybrids between two species is at least strongly suggestive of a common ancestry at no very remote time.

Maize and annual teosinte have long been known to hybridize freely and naturally if given the opportunity, and the hybrids are fertile. Perennial teosinte has been hybridized with maize, but the hybrids show a much lower degree of fertility.

Attempts to hybridize maize and *Tripsacum* met with failure until special technique was employed by Mangelsdorf and Reeves (1931). Observing that the pollen of *Tripsacum dactyloides* germinated on the stigmas of maize and that the pollen tubes entered the styles, they assumed that the tubes were not able to grow the length of the styles of maize and assist in the formation of seeds. Accordingly, they cut back the styles of maize to about the length of those of *Tripsacum* before applying the pollen of *Tripsacum*. A small percentage of the pistils thus treated set seeds, and a few of these germinated, producing plants much like *Tripsacum* in appearance, but evidently hybrids. The mechanical difficulty involved in this process and the small number and low vitality of seeds produced certainly preclude any probability of the natural hybridization of these species.

Collins and Kempton (1916) made a number of attempts to hybridize *Tripsacum* with maize and with teosinte but were unsuccessful in almost all cases. One pollination of *Tripsacum* with maize, however, produced plants like the female parent; and from a pollination of teosinte with *Tripsacum* one plant was secured which resembled the male parent in every detail. For the latter genetic phenomenon they coined the word *patrogenesis*. Since these results have not since been substantiated, neither the new genetic term nor their assumption, that in the one case an egg, and in the other a sperm, developed without sexual union, need be given serious consideration.

No hybrids between *Tripsacum* and any of the *Rottboellieae* have been reported, and it is probable that no attempt has been made to hybridize them.

Inflorescences

If we disregard for a moment the inflorescence of maize, the interpretation of whose peculiarities has been the central problem of all recent studies of the ancestry of the plant, it is not a difficult matter to detect a consistent homology in the inflorescences of *Euchlaena*, *Tripsacum*, and the *Rottboellieae*.

In these grasses the inflorescence consists of one or more spike-like structures, each made up of a rachis bearing two rows of pairs of spikelets in alternate arrangement (Figs. 6-10). This unit is the end product of two great lines of evolution which are evident in all the higher grasses, and which have been recognized, vaguely at least, in modern systems of classification of the family.

Paired Spikelets.—One of these evolutionary tendencies has been toward the aggregation of spikelets into definite, stable groups, with the subsequent high specialization of the group. This end has been attained to some degree in several genera of other tribes, such as *Olyra, Pharus, Lithachne,* and *Leptaspis,* and in all the *Andropogoneae* and *Maydeae.* The unit ultimately reached is ordinarily a pair of spikelets, but groups of three regularly occur in a few cases, and irregularities occur sporadically in many genera.

This pair of spikelets has superficially a contradictory aspect, for it would seem that its two members were two branches arising from one node of the rachis, a thing which does not ordinarily occur in the grasses. A close examination of the manner of insertion of the two spikelets, however, shows that the two are really borne on a single short branch which arises from the node. This is clearly shown in some cases in which the unit is distinctly stalked, and occasionally in a single inflorescence a series may be selected which will represent all the steps in the theoretical evolution of the pair of spikelets from a short branch of an ordinary panicle. Such studies as have been made of the vascular connections between the rachis and the spikelets also substantiate this interpretation.

It seems certain that similar groupings of spikelets in other tribes of grasses have come about by parallel but independent lines of evolution. Illustrations are seen in the short, deciduous branches of *Aegopogon, Bouteloua,* etc., the peculiar clusters of spikelets in *Tragus, Anthephora,* and *Bulbilis,* the variously differentiated triads of *Hordeum,* and even in the involucrate clusters constituting the burs of *Cenchrus.*

Differentiation in the Pair of Spikelets.—In the *Andropogoneae* and *Maydeae* the spikelets probably reached the paired condition with one sessile and the other pedicelled, and each containing two florets. Since then there has occurred a progressive suppression of parts, the lower floret of the spikelet tending to disappear before the upper, and the pedicelled spikelet preceding the sessile. This has resulted in several typical conditions, the following of which are of interest:

1. Sessile spikelet with the upper flower perfect, the lower floret represented by only the lemma; pedicelled spikelet with the upper flower staminate and the lower reduced to the lemma, or the whole structure reduced to only the pedicel: the *Rottboellieae.*

2. Each spikelet containing two staminate flowers: staminate inflorescence of maize and teosinte and staminate portion of inflorescence of *Tripsacum.*

3. Sessile spikelet with one pistillate flower, the lower floret represented by the lemma and palea; pedicelled spikelet represented by a microscopic rudi-

ment: pistillate part of inflorescence of *Tripsacum* and pistillate inflorescence of teosinte.

4. Both the spikelets almost sessile, each having one pistillate flower and the lemma and palea of the other floret: pistillate inflorescence of most kinds of maize.

5. Both spikelets almost sessile, each having two pistillate flowers: a few varieties of maize.

All these types are replete with microscopic vestigial organs suggesting the generalized ancestral form. A restoration of the parts whose loss we can reasonably assume from a comparative study of all these types would give us the pair of two-flowered spikelets, a combination of characteristics which does not occur functionally in any known genus, but every lost organ of which is fully accounted for somewhere by a rudiment. This is as near conclusive evidence of the course of evolution as we can secure by means of comparative morphology.

In the plants in which the ontogeny of these vestigial parts has been studied they develop like their functional homologues up to a point more or less characteristic of the species, where they stop, remain static for a time, and then slowly deteriorate. Often enough to be suggestive they may continue to develop, proceeding even to functional maturity and thus making the spikelet resemble a little more closely the theoretical ancestral type.

The Spike or Raceme.—The second great line of evolution culminating in the inflorescences of these grasses has consisted of the reduction of a loose panicle to one or a few spike-like aggregations of spikelets. This process and the other, by which the spikelets were paired, have evidently been carried out independently, for there are loose panicles in which the spikelets are paired (*Olyra, Lithachne, Sorghum, Sorghastrum,* etc.) as well as spike-like branches on which they are not paired (*Chloris, Elusine, Panicum, Paspalum,* etc). Both results have been accomplished in the *Maydeae* and in many of the *Andropogoneae.*

Terminology.—For these ultimate spike-like aggregations of paired spikelets botanical terminology has no entirely appropriate name. In fact, it is only after a liberal expansion of definitions that we can make any of the common terms used in designating types of inflorescences apply to those of the grass family. At the very beginning we take the liberty of substituting the spikelet for the flower and applying to clusters of *spikelets* the terms ordinarily applied to similar clusters of *flowers.*

When we say, then, that the inflorescence of *Panicum, Poa, Festuca, Bromus, Sorghum,* or *Oryza* is a panicle we mean that it is a panicle of spikelets. In a strict sense, however, this is inaccurate if we limit the term *panicle* to an indeterminate inflorescence. The grass inflorescence is neither determinate nor indeterminate; differentiation in the whole structure or any of its branches begins neither at the base nor at the tip, but somewhere between, and proceeds simultaneously in both directions.

The more strict units of inflorescence in maize and its relatives involve an

additional difficulty. If they were as simple as they seem to be, the words *spike* and *raceme* would, without further qualification, serve to designate them. But their simplicity is a derived one, due to a very definite specialization, and they fall into a very different category from that which includes the simple spike and raceme.

Confronted with this inadequacy of language we can do one of two things: we can create new words to express more explicit distinctions, or we can grant to existing terms broader, if less accurate, application. The latter is doubtless the lesser of the two evils, and it is in conformity with a usage already established under conditions which failed to recognize its inconsistency.

The term *spike* will, then, apply to those units of inflorescence in which the spikelets are sessile on a common rachis. When any or all of the spikelets are pedicelled, the structure is a *raceme*. A compound inflorescence, in which the spikelets are borne on subdivisions of the primary branches, is a *panicle*.

Forms of Inflorescence.—In those *Andropogoneae* most like *Tripsacum* the inflorescence consists of one or more spikes or racemes. The sessile spikelet contains one perfect flower, and the pedicelled spikelet may have a staminate flower or may be only a functionless rudiment (Fig. 8).

Similar spicate or racemose structures, occurring singly, in pairs, or in digitate clusters, make up the inflorescence of *Tripsacum*. (Fig. 7). Here, however, the lower part of each unit is pistillate and the upper part staminate. The pistillate spikelets, each accompanied by a rudiment representing the pedicelled member of the pair, are arranged alternately in two rows and partly imbedded in the sides of the rachis. The staminate spikelets are paired, with one member sessile and the other sessile or pedicelled.

Sexual differentiation is more pronounced in *Euchlaena,* most of the inflorescences being unisexual (Fig. 6). The staminate inflorescences, which terminate the main culms, are each made up of racemes similar to the staminate parts of the inflorescence of *Tripsacum*. The pistillate spikes occur singly or in simple digitate groups borne alternately on compound lateral branches which are so short that the inflorescences usually remain enclosed in the subtending sheath until after the flowering (Fig. 9). In essential structure these spikes are similar to the pistillate parts of the inflorescence of *Tripsacum*. Mixed inflorescences also frequently occur, the pistillate and staminate parts being arranged as in *Tripsacum*.

Sexual Differentiation.—In the species of grasses which have imperfect flowers each male or female flower has aborted organs of the opposite sex; and during development the suppression of these organs occurs in a definite and orderly way. In most monoecious species also the staminate and pistillate spikelets are arranged in definite ways on the axes, and we know that differentiation in any one axis begins at a more or less definite place and proceeds toward both ends. The synchronization of these various gradients of formation and development is apparently the thing which determines the ultimate sex of any particular flower, and it is evident that our present knowledge of the quantitative aspects of the various factors does not permit a complete explanation.

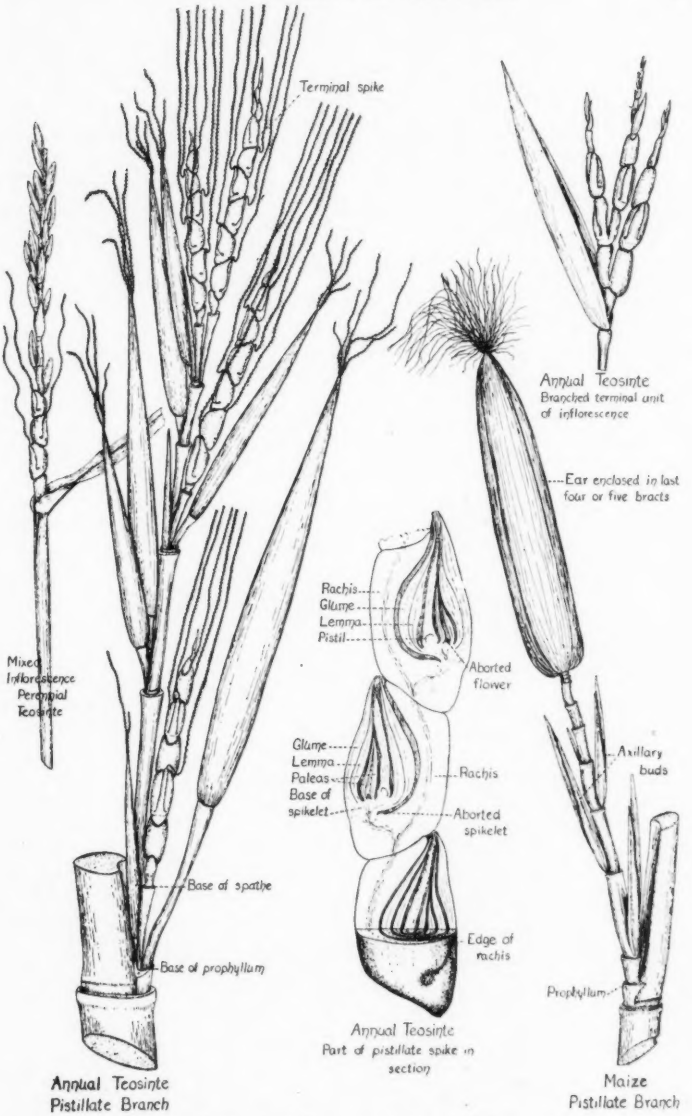

Fig. 9. Pistillate inflorescences of *Zea* and *Euchlaena*.

It does seem, however, that the difference in sexual condition between *Tripsacum* and *Euchlaena,* and between them and *Manisuris,* is fundamentally physiological, and that the evolution of one condition from another consists essentially of a shift in one or more gradients, just as sporadic sexual anomalies or experimentally produced sex reversals represent temporary shifts due to critically modified factors of environment.

The Ancestral Type.—A common stock from which all the plants under consideration could have been differentiated by the mere suppression of parts would necessarily have spikelets as primitive in form as those of *Isachne,* one of the most primitive of the *Paniceae.* In this genus the spikelet has two perfect flowers, but the spikelets are not paired. Other correlated characteristics would, however, lead us to expect a closer source of unity than this would imply. The frequence and apparent facility with which the aborted parts may be restored to function also suggest a recent differentiation, although the strict mutationist may not particularly care for this kind of evidence. It seems more plausible to assume, therefore, that the two-flowered condition of the staminate spikelets of the *Maydeae* and of the pistillate spikelets of some varieties of maize represent a permanent reversion to an earlier condition rather than the independent retention of a primitive characteristic through a long period of evolution.

Many consistent pictures of the relationships under consideration might be drawn, but the one which at present seems best has a branch of the Andropogonean stock separating into two parts, one of which has the combination of gradients leading toward monoecism, while the other has not. The former becomes the progenitor of the *Maydeae* and the latter of the *Rottboellieae.*

Fig. 10. Staminate inflorescence of maize.

A further division of the Maydean stock gives rise to two lines, one of which culminates in the various species of *Tripsacum,* while the other divides to produce maize and teosinte. An alternate view, that the line representing *Tripsacum* and the one producing maize and teosinte separated independently from the perfect-flowered stock, would be almost as easy to defend.

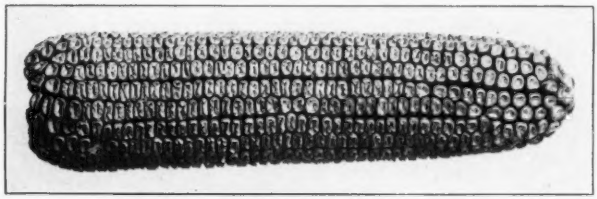

Fig. 11. A "normal" ear of corn.

The Ear of Maize

The inflorescences of maize are so well known and have been so fully treated that a description of only certain significant features is necessary. In the lateral branches of the staminate tassel the pairs of spikelets are usually arranged alternately in two rows, as they are in the other *Maydeae* and in many of the *Andropogoneae;* but occasionally in these lateral racemes, and ordinarily in the central raceme of the tassel and in the pistillate inflorescence, the pairs of spikelets are arranged in four or more longitudinal rows (Fig. 10).

In maize plants grown on poor soil, or developed late in the growing season, or in varieties whose vigor has been attenuated by inbreeding, pistillate inflorescences are frequently found in which the pairs of spikelets are arranged in two rows, and the same feature is likely to be duplicated in the central raceme of the tassel; but under ordinary conditions there is no indication of the distichous structure in these parts of the inflorescence.

The organization of the pistillate inflorescence is so faithfully expressed in the mature fruit that, for purpose of analysis and interpretation, the problem may well be resolved into an inquiry into the structure and significance of the well known "ear" of the plant. This exhibits a wide range of variation, but the features which are thought to mean most in determining the course followed in its evolution can be brought out in a description of a relatively small number of types.

The Ordinary Ear.—The ear of corn most commonly encountered today, and which has apparently been the ideal of the breeder through the centuries, is made up of a cylindrical "cob" around which the grains are arranged in eight or more parallel longitudinal rows. (Fig. 11). These rows are grouped in pairs because the spikelets are in pairs, two grains, one from each row, being attached to the cob by a short stalk. That this interpretation of the paired grains is a matter of reality, and not merely theoretical, is readily shown by the ease with which a pair of grains may be detached from the cob as a

unit by cutting the common peduncle (Fig. 13, B). The grains are so large that they protrude far beyond the dwarfed bracts of the spikelets, and the latter form the chaffy covering of the cob after removal of the grains.

Depauperate Ears.—Inasmuch as the pairs of spikelets always occur in at least two rows, and both spikelets develop grains, an ear cannot ordinarily have fewer than four rows of grains; and even these occur only as a result of the unusual conditions previously mentioned which decrease vigor.

In an experiment designed to test the effect of extreme starvation on a small, normally eight-rowed variety, four-rowed ears have been commonly produced; and it has been possible to reduce the length of the ear almost to the vanishing point without the loss of either grain of the pair except at the distal end of the ear, where one spikelet of the last one or two pairs becomes staminate or abortive (Fig. 12).

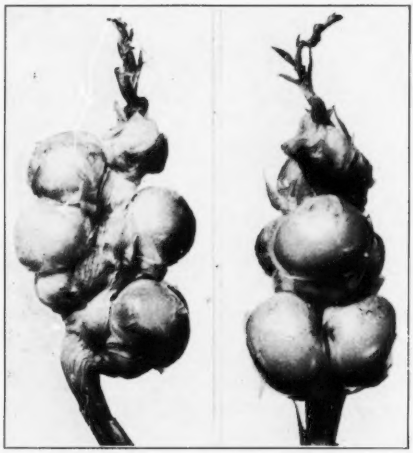

Fig. 12. Two views of an ear of corn from a poorly-nourished dwarf variety.

This persistent retention of both spikelets of the pair in the pistillate inflorescence sets the maize plant apart from all other members of the *Maydeae*. Although both spikelets may occasionally be fully developed in *Tripsacum*, *Euchlaena*, or some of the Oriental *Maydeae*, we must go to some of the most primitive *Andropogoneae*, such as *Imperata*, *Miscanthus*, or *Saccharum*, to find the regular production of fruits in both members of the pair.

Variation in Number of Rows.—Since the pairs of spikelets may develop in any number of rows from two upward to 10, 12, or more, ears with from six rows upward are possible. Six-rowed ears are rare, eight rows are common in many varieties, and higher numbers, in multiples of two, up to 24 rows or more, may be found in some of the more productive dent varieties.

Irregular Arrangement of Grains.—In some varieties, particularly in Country Gentleman sweet corn, the grains do not appear in regular rows, and it would appear that the regular linear arrangement of spikelets had been lost (Fig. 13, A). But if the grains are removed from such an ear and the chaffy bracts of the spikelets cut away, the peduncles of the pairs of spikelets are found to be in straight rows. The real cause of the irregularity is seen in the spikelets themselves. The lower flower of each spikelet, which is usually aborted in other varieties, has in some way partially or completely regained its function, and each primary branch of the ear may produce as many as four grains instead of the usual two.[31] This possibility is seldom completely expressed throughout the ear, and the pair of spikelets may have from one to

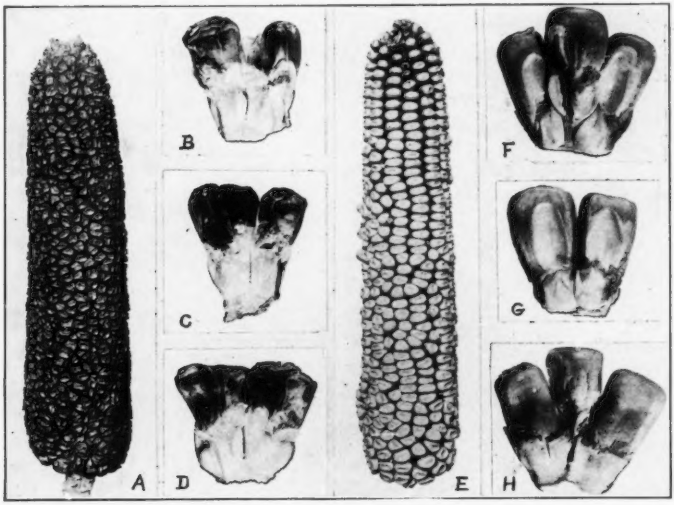

Fig. 13. Ears with irregular rows of grains. A, ear of country gentleman sweet corn; B-D, primary branches of same with grains in 2's, 3's, and 4's. E, an ear in which some primary branches have grains in 3's; F-H, primary branches of same.

four grains, with three or four predominant (Fig. 13, B-D). This irregularity in the structure of the primary branch, with the crowding brought about by the presence of the supernumerary grains, effectively breaks up the linear arrangement which would otherwise prevail.

Another type of irregularity in the rows of grains is due to the grouping of spikelets in threes rather than in pairs (Fig. 13, E). In at least one variety of dent corn grown in Illinois this peculiarity occurs to such an extent as to

31 Stewart (1915); Weatherwax (1918).

impair the value of the ears for show purposes.[32] Although it seldom occurs in more than 10% to 15% of the possible number of times in any one ear, it is evidently inherited, environmental conditions doubtless being responsible for its erratic appearance. The extra grain of the group, which is usually between the other two, stands conspicuously higher than the others because the spikelet which produces it is pedicelled (Fig. 13, F, H). If all the spikelets in an inflorescence were in threes, and all produced grains, we should have the interesting possibility of an ear with an *odd* number of rows of grains whenever the groups appeared in an odd number of rows. No other native American species of the *Maydeae* has its spikelets in triads, but this grouping is the regular thing in *Coix*,[33] is found regularly at the ends of the branches of the inflorescence in the sorghums, and occurs occasionally in other places in the inflorescences of other members of the *Andropogoneae*.

Dropping of Rows.—The rows of grains on an ear usually extend from the base to the tip, but specimens are sometimes found in which some rows extend only part way (Fig. 14, A). In such cases the total number of rows at the base may be two, four, six, or even more, in excess of the number at the tip. This difference seems externally to have come about by the dropping of one row from each of two or more pairs as the inflorescence was being formed, and one author has assumed that one member of each pair of grains is

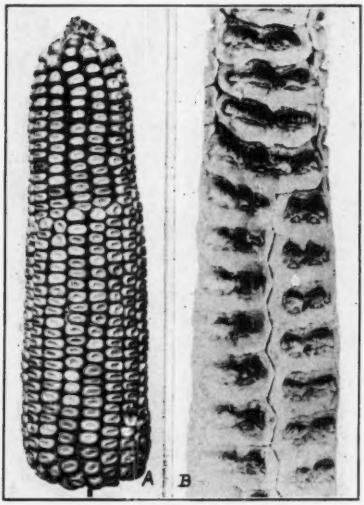

Fig. 14. Discontinuance of rows between base and tip. A, an ear with 18 rows at base and 14 at tip; B, cob of a similar ear, with chaff removed to show the dropping of a row of primary branches.

32 I am indebted to Floyd Carter, of Gridley, Illinois, for excellent material showing this peculiarity.

33 Weatherwax (1926).

dropped for a part of the length of the ear.[34] But, as in other cases of such irregularity, the external appearance does not accurately indicate the structure. Removal of the grains and chaff from the cob shows (Fig. 14, B) that one or more entire rows of paired spikelets have been discontinued.[35] In view of the influence exerted by starvation experimentally produced, it may be inferred that this change in the number of rows is due to a decrease in nutrition during development. The rare instances in which the number of rows toward the tip of the ear is greater than the number at the base may be due to a nutritional change in the opposite direction.

Sex Reversals.—The ear ordinarily develops from an inflorescence which is essentially pistillate, but not uncommonly some of the flowers may be staminate or perfect. Some of these anomalies are hereditary, and some can be

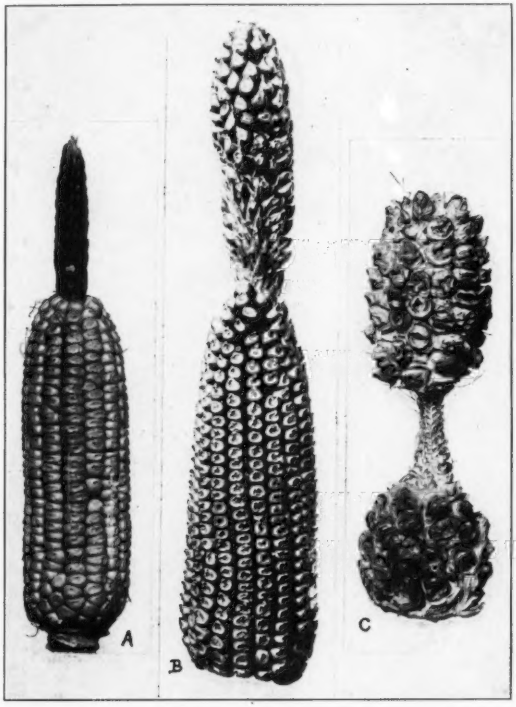

Fig. 15. Ears with staminate or aborted parts. A, staminate tip; B, staminate middle portion; C, aborted middle part.

34 Collins (1919c).
35 Weatherwax (1920).

attributed only to fluctuations of environment. When the flowers are perfect, the stamens develop to their normal size instead of remaining rudimentary. Sometimes the staminate flowers are in spikelets which have assumed the complete staminate form. These may be aggregated in a definite part of the inflorescence, as when a portion of the ear is transformed into a staminate raceme like the central raceme of the tassel (Fig. 15, A, B), or they may be scattered at random throughout the length of the ear. In the latter case usually only one member of the pair of spikelets is affected, and the resulting staminate spikelet becomes pedicelled. The same arrangement of a sessile pistillate and a pedicelled staminate spikelet in a pair is frequently found at the border line between the pistillate and staminate parts of the more definitely differentiated inflorescences.

Probably closely related in cause to some of these sexually transformed ears are others in which the tip, or more rarely an intermediate part, has suffered, early in development, some physiological effect which has caused the cob and its spikelets to remain abortive (Fig. 15, C).

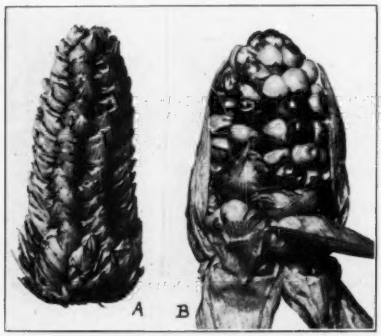

Fig. 16. A, an ear of pod corn; B, teopod corn.

Pod Corn.—A bizarre anomaly, which never fails to arouse interest, is the variety known as pod corn (Fig. 16, A). In this the six bracts of the spikelet, which are usually abortive, develop to such an extent that they cover the grain, or pair of grains, produced by the spikelet. These bracts may be short and firm and closely applied to the grain, or they may be softer and more foliaceous, and much longer than the grain. Podded ears also have the additional husks of ordinary ears.

Teopod Corn.—Similar to pod corn in appearance is a variety which has been called teopod corn because the grains are covered with husks and the plant as a whole has some resemblance to teosinte.[36] The bracts which cover the grains, in addition to an unusually large number of ordinary husks, are, however, not the equivalent of those of pod corn. Each is a bract on the main axis of the ear with above it a primary branch bearing two grains (Fig. 16, B).

36 Lindstrom (1925); Weatherwax (1929).

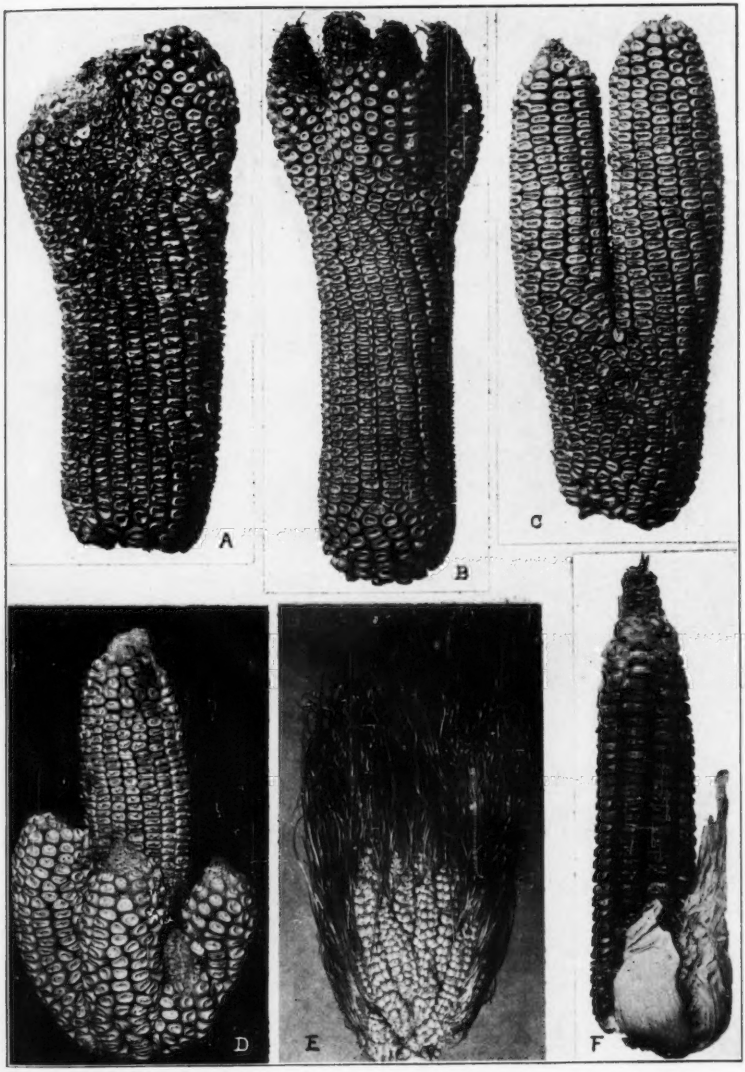

Fig. 17. Branched ears. A-C, types of fasciation or branching at tip; D, whorl of branches at base; E, branch corn; F, pair of spikelets modified into ear-like branches.

Branched Ears.—The ears thus far described are really paniculate in structure because the spikelets are borne on branches of the main axis rather than on the axis itself; but these primary branches are so short that the whole structure is spike-like in appearance. There are, however, a number of other types of ears in which the paniculate form is more evident in one way or another.

A variety known as branch corn[37] has an ear in the form of a loose panicle resembling the fruiting panicles of some of the sorghums (Fig. 17, E). The grains, however, are paired as in ordinary ears, whereas in the sorghums only one spikelet of each pair produces a grain. The staminate inflorescence of this variety also lacks the strict, spike-like terminal portion characteristic of most other varieties, and many of the spikelets are not definitely paired.

Another variation in which the strict unity of the ordinary ear is more or less broken up is seen in a series of forms ranging from cases of fasciation to a definite division of the terminal part of the ear into two or more ear-like branches (Fig. 17, A-C). The fasciated condition is inherited in some varieties. Whether hereditary or not, the origin of these anomalies is to be attributed to a malformation or division of the growing point during the development of the inflorescence.

There are at least three ways in which branches may be produced at or near the base of the ordinary ear, and each of these ways involves a matter of degree of development of some structure already accounted for in homology.

The least confusing of these is the type in which the buds in the axils of the husks develop as small ears. This occurs occasionally in almost any variety and somewhat regularly in many. It is a vegetative characteristic more properly than a peculiarity of the inflorescence.

Another type of fruit has one or two or a whorl of branches around the base of an ear otherwise of the ordinary form (Fig. 17, D). Each of these branches usually has four rows of grains, but in some cases there may be eight or more. Some forms of the peculiarity are known to be inherited, but in many cases no such cause can be assigned. This form of the ear is almost an exact homologue of the ordinary staminate inflorescence. It is not to be confused, however, with similar structures borne at the ends of basal tillers. The inflorescences of the latter are extremely variable, and suggestive series between the ordinary staminate and pistillate inflorescences can be selected from among them; but they do not necessarily tell the same story as do these branched ears borne in the normal position.

The third type of basal branching, frequently seen in sweet corn, but known also in other varieties, has one or more small ears, each surrounded by husks, attached near the base of an ordinary ear (Fig. 17, F). There may be more than one form of this peculiarity, but in the five or six specimens that I have had opportunity to examine, the small ear-like structures fall into a cate-

37 Gernert (1912).

gory of structures which develop in places where spikelets would be expected, and doubtless from spikelet primordia. I have described (1925) some of these which were produced at the base of the staminate inflorescence. There are two good evidences that these branches are modified spikelets. Each of them usually has six husks, corresponding to the six bracts of the spikelet; and the structures themselves occur in pairs. Where they sometimes seem to occur singly, a close examination usually reveals the other member of the pair as a small staminate spikelet or a rudiment. Two anomalies which Kempton has mentioned (1921) apparently belong in the same class, although he did not recognize the homology.

The Normal Ear.—In view of all this diversity of form in the inflorescence of maize some interesting questions arise. Which of all these is to be regarded as the *normal* ear, and what does the word *normal* mean in such an application? Just where and in what manner does this inflorescence connect most satisfactorily with the rest of the grass family? What kind of ear represents most nearly that of the plant which the Indian first placed under domestication, and what significant evolutionary progress has been made under cultivation? To what extent and in what manner can we safely utilize this variation in the structure of the ear toward building up a picture of the past?

When we speak of a *normal* structure or condition in a plant we probably have reference to some more or less constant and persistent type which appears with relatively high frequenty generation after generation, and we regard as abnormal the things which deviate perceptibly from this concept. It follows, then, that in a consideration of the course of evolution leading up to a thing which shows marked variation, the determination of the normal is a matter of some importance, and it can often be detected only by the application of mathematical methods.

If all the ears of corn in the world at any one time could be considered biometrically, the ear which has been described as the approximate ideal of the breeder would probably turn out to be something near the normal structure; and all evidences from history and archeology indicate that the result of any such study would have been much the same at any time during the past five hundred years. But would the statistical method be pointing out to us a type which is persisting because of its fundamental biological significance? In other words, does the frequency of this kind of ear today justify our assuming that it is the best indicator of the course of evolution?

The far-reaching effects of centuries of conscious selection in a species like this, where the individual plant has received so much attention, and the large numbers in which the standardized ear is produced today raise some doubt as to whether the ear which we regard as normal is any more significant as an indicator than are some of the less frequent forms. In fact, the aboriginal farmer who first domesticated the corn plant may have started with what would then have been, when evaluated statistically or genetically, an *abnormal* type of ear, and his care and protection may have given this type today a prominence that it would never have had under natural conditions.

Theories as to the Origin of the Ear

Regardless of the status which we may assign to any one of these various types of ear as normal or abnormal, the fruit of maize represents a divergence from the typical plan of structure of the grasses in that it consists of an axis bearing many longitudinal rows of lateral appendages. Throughout the grass family, with the possible exception of a few tropical genera which have apparently departed on evolutionary experiments of their own, the vegetative axes have their leaves and branches arranged alternately in two rows, and the same arrangement can be recognized in most types of inflorescence.

The distichous plan is so well established here that the polystichous arrangement in the inflorescence of maize has been regarded as almost a unique innovation which required some sort of explanation. It seems probable that the ear in all its forms has evolved from an inflorescence which was built on a distichous plan, and the mutation, or series of mutations, responsible for this modification of structure is a step of special interest in the evolution of the plant. The cause of this change is as obscure as that of mutations in general, but we should hope to be able to detect a homology between the old form and the new. That this relationship is not easy to detect is shown by the divergence in the theories which attempt to explain it.

The Staminate Homologue.—Investigation of this problem from the evolutionary standpoint has proceeded for some time before it was clearly pointed out that the ear is exactly like the terminal raceme of the staminate tassel (Fig. 10) in essential structure, except for such divergences as are closely associated with the difference in function.[38] This eliminated the lateral racemes of the staminate inflorescence from any place in the homology except as their equivalents appear as a basal whorl in anomalous ears (Fig. 17, D). But the recognition of this homology does not solve the problem, for the terminal raceme of the tassel is seen to be as difficult to explain as is the ear.

Origin by Contraction of a Panicle.—Equally ineffectual on final analysis is the theory that the ear was evolved from a loose panicle by the shortening of numerous branches until each remained as only a pair of spikelets.[39] For a time the weakest point in this theory was thought to be the lack of direct evidence that such contraction of branches had ever taken place, but branch corn supplies material from which a suggestive series of branches illustrating the reduction can be selected.[40] This seems to be a satisfactory way of explaining the origin of the pair of spikelets as well as the spicate branches which make up the inflorescences of many grasses; but it gives no clue as to how the parts in the ear of corn came to be arranged in many rows instead of two rows, which is the essential question.

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38 This homology was cited as early as 1854 by Wigand (1854) and was considered by Goebel in his study of grass inflorescences in 1884. Its bearing on the ancestry of the plant was pointed out by Mrs. Kellerman (1895) and was discussed in more detail by Montgomery (1906) and Collins (1912).

39 This explanation, first advanced by Collins (1912, p. 526), was suggested to him by F. V. Coville.

40 Weatherwax (1918) p. 328.

Origin by Twisting of a Spike.—Another way of explaining the many-rowed inflorescence has been suggested by the ears of second-generation hybrids between maize and teosinte. In a population produced by self-pollenizing a hybrid between these species many different kinds of pistillate inflorescences are produced, and these may be arranged in a graded series from some closely resembling teosinte to others much like maize.

Collins (1919) has examined such series and concludes that they illustrate all the steps that would be necessary in changing a spike like that of teosinte to a structure like the ear of maize. These steps are pictured as follows:

1. The suppressed spikelet of each pair reappears in staminate or pistillate form, but ultimately becomes pistillate.

2. The internodes of the rachis become shorter and increase in number, and the pairs of spikelets become crowded.

3. Adjacent internodes become "yoked" together in pairs so that a new structural unit comes into existence as a transverse member bearing at each end a pair of spikelets.

4. By a twisting of the axis these "yokes," which were at first in one plane, become turned so that they stand at various angles to one another, and thus the number of spikelets in the circumference is increased.

There is no implication in this theory that the ear of corn originated from the spike of teosinte. It is only an explanation of a manipulation by which the change from distichism to polytichism might have taken place.

To find in an ordinary ear of corn some evidence of this "yoking" of a pair of spikelets on one side with another pair diametrically opposite would greatly strengthen this interpretation. Collins believes that he finds this in ears which have more rows at the base than at the tip; he states (1919c, p. 133) that "there is abundant evidence to show that rows are usually interrupted by the abortion of the pedicelled spikelets only." He further says that at the same time at which the pedicelled spikelets of a row of pairs on one side of the ear are aborted the same thing occurs in a row of pairs diametrically opposite, this concordant behavior being due to the hypothetical "yoking" of pairs through the axis.

Collins does not elaborate on this observation, and it is difficult to see how he arrived at such conclusions by the application of morphological technique, for the facts are really quite to the contrary. He may have judged wholly from the external appearance of mature ears, but, as has alreay been explained,[41] basic irregularities in structure are seldom accurately reflected in the surface appearance. The removal of the chaff from the cob, until the bases of the pairs of spikelets are exposed, shows the true arrangement of the grains. When rows of grains are dropped between the base and the tip of the ear, it means that a row of pairs is dropped rather than that one spikelet of each pair is dropped from each of two rows. As a matter of fact, the abortion of either member of a pair of spikelets in maize, in either the staminate or the pistillate inflorescence, is a thing of rare occurrence.

41 See p. 33 and Weatherwax (1920).

This "yoking" of adjacent internodes in the inflorescence of hybrids of maize and teosinte is a peculiar anatomical characteristic which should be better understood. I believe that it might be possible to show a connection between it and the occurrence of long and short internodes in alternate sequence in the vegetative parts of some grasses, such as *Cynodon dactylon, Stenotaphrum secundatum,* and species of *Chloris,* by means of which the leaves are made to appear in almost opposite arrangement, and I think that this may be an expression of a type of dorsiventrality which is known to occur in the culms of grasses. But I see no indication of such association of parts in an ear of corn and know of no way in which this principle can be used in interpreting this structure.

The Fusion Theory.—Probably the oldest, and certainly the most widely accepted theory explaining the structure of the ear of corn, pictures it as having been formed by the fusion, side by side, of a number of units like the two-ranked spikes or racemes of closely related grasses or the branches of the staminate inflorescence of maize itself.

As far as I can learn, this idea was first clearly stated by Hackel in 1889, but it was probably current in an indefinite form before this. It has since received at least partial sanction from many other investigators.

There are many facts which make this explanation seem especially plausible. Each two adjacent rows of pairs of spikelets are often separated by what looks like a line of fusion, and when a cob is subjected to physical stress or begins to decay on exposure to the weather, it frequently splits along these lines. The crowding of grains sometimes causes the cob to split in the same way as the ear approaches maturity or as it dries after maturity; and one hereditary form of "branching" in the ear looks, from the published figure,[42] very much like the same thing, but the description does not include sufficient morphological detail for a full interpretation. The branches of the tassel are packed together during development in a way which suggests the ease with which they might fuse into a single unit, and it might seem all the more reasonable for fusion to occur in an inflorescence like this which does not emerge from its covering of leaf sheaths. Variously branched or fasciated ears appear often enough to give apparent support to the theory, and ears which show a loss of rows toward the tip might be understood as having incorporated in their make-up one or more branches shorter than the others.

Notwithstanding the wide acceptance and seemingly reasonable nature of the theory, there are certain points of fundamental significance which it overlooks or ignores, and a consideration of which practically invalidates it.

Mathematical Inconsistencies.—There is no general agreement as to the nature of the structures which are thought to have fused to form the ear. The ordinary statement is that they were like the lateral racemes of the staminate inflorescence. But each of these bears *pairs* of spikelets in *two* rows, altogether four rows of spikelets. A four-rowed ear would consist of one of these units, an eight-rowed ear of two, a twelve-rowed ear of three, etc.; but it is difficult to see how four-rowed units could combine in such a way as to

42 Kempton (1923), fig. 4, p. 249.

produce ears with ten, fourteen, or eighteen rows, all of which frequently occur. Different investigators who have supported the fusion theory either are unaware of this inconsistency or evade it in some way.

Hackel says (1890, p. 38) that each pair of rows corresponds to a single spike of Euchlaena, and the same idea has been expressed by others in later years. But it will be remembered that the rows of grains in maize are paired because the spikelets are paired, while the fruits of teosinte are in two rows because of the distichous arrangement of the spikelets on the rachis, one member of each pair being aborted. Spikes like those of *Euchlaena* or *Tripsacum* could, therefore, in no way fuse to form anything like an ear of maize unless the aborted spikelet should become functional; and in that case the spike would contribute four rows of spikelets to the structure being formed.

Kempton (1919) attempts to reconcile the mathematical inconsistency of the fusion theory but apparently does not understand the morphological criteria for the evaluation of aborted structures in forming a theory of evolution. He says (p. 7):

> . . . , there is really no mathematical difficulty involved in developing ears with ten, fourteen, or eighteen rows by the fasciation of 4-rowed branches. Ears having rows in these numbers can be obtained by the abortion of a row of paired spikelets or the abortion of the pedicelled spikelets of one of the component branches, both of which phenomena are of rather frequent occurrence.

The mathematical part of this statement is obviously correct. If we grant that such abortions occur, this part of the problem is solved. But Kempton cites no evidence whatever in support of his statement that such abortions do occur frequently. It is true that almost anywhere on an ear one spikelet of a pair may become staminate, and it may even be reduced to a functionless vestige; but the ears which cause the trouble for this theory have undergone no such reduction, as proper dissection readily shows. I am unaware of any evidence that a row of pairs of spikelets is ever aborted, in the sense implied, and such an abortion would, if it occurred, constitute a most peculiar morphological phenomenon, affecting alternate lateral members of an axis. Vestigial organs provide a most valuable means of reconstructing the past history of a plant; in their origin and early development, and in the method of their decline, they give positive evidence of homologies, and we have but to put them into the picture as functional units to see the past. But we must first find the vestiges.

Kempton further predicts (1919, p. 7) that a statistical study would show that varieties with rows in multiples of four are more common than those with rows in other numbers. It is questionable, however, whether, for this purpose, much weight can reasonably be given to a statistical analysis of a population that has undergone as much conscious, and biologically capricious selection as has the ear of maize. A mathematical principle of this kind, moreover, is invalidated by relatively few inconsistencies, and the qualitative fact that it is possible for ears with these perplexing numbers to occur at all is enough to offset the quantitative aspect.

Worsdell (1916, p. 58) assumes that the ear represents a fusion of "nu-

merous spikes with flattened rachis, each bearing two rows of female spikelets," but warns against the application of the term *fasciation*. As a structure resulting from the fusion of axes it is, he says, apparently unique in the plant kingdom. He proceeds then to describe briefly an "abnormality" in which the ear is represented by a paniculate inflorescence resembling the staminate tassel. This step is regarded as a reversion, and he calls it *disruption*. It is interesting to note that, although he has the ear originally formed by the fusion of *two*-rowed spikes, the exact like of which, incidentally, does not occur in any grass inflorescence, he has it "disrupt" into an *eight*-rowed central spike surrounded by a number of *four*-rowed spikes.[43]

The Nature of Congenital Fusion.—An examination of the general principle of the origin of organs by the fusion of more simple parts brings to light some other difficulties incident to its application to the problem at hand. There are undoubtedly numerous instances in the plant kingdom in which a single structure now embodies the essentials of what once consisted of two or more structures; and we commonly say that the parts have fused. Examples are afforded by the compound ovary, inferior ovary, gamopetalous corolla, perigynous stamens, etc. of the more highly specialized Angiosperms. There are cases, too, in which even separate axes have fused in this way, as in the bur of *Cenchrus*, where a number of branches have joined side by side to form an involucre, or in the pistillate portion of the inflorescence of *Polytoca* or *Chionachne*, where the pedicel of an aborted spikelet, which is a branch of the rachis, has fused for a part of its length with the rachis itself.

What do we mean when we say that the parts have *fused* in these instances? Do we mean that in the development of each individual plant today the parts are at first separate and later unite laterally? Or do we mean that, at some time in the past, parts which were separate united during the ontogeny of some one individual and the anomaly was hereditary thereafter? We probably mean to imply neither of these things, but, rather, that in each case a certain group of discrete organs came, gradually or suddenly in the phylogeny of the race, to be replaced by a single organ comprising material homologous with that which had before been represented in the separate organs. Fusion, then, is a concept of phylogeny rather than a fact of ontogeny, and when so qualified the term probably expresses accurately what has happened in some instances.

Fusion and Fasciation.—Many who have attempted to apply the fusion theory to the ear of corn have treated *fusion* and *fasciation* as synonymous terms. The typical case of fasciation, as seen occasionally in the stem of *Ipomoea*, the peduncles and heads of many composites, the flowers of some varieties of tomatoes, etc., is a flattened structure resembling two or more structures grown together. Worsdell points out, however, that this is a case of incomplete separation rather than one of union. A fasciated structure, then, is to be regarded as a simple organ that has made an unsuccessful attempt to branch, rather than a compound structure produced by the fusion of branches which were once separate. It follows that probably no one who has

43 As shown by Ascherson's figure which Worsdell copies in his fig. 13, pl. 39.

called the ear of corn a fasciated structure has really had in mind this meaning of the term.

No Evidence of Fusion.—Any organ which is generally regarded as having arisen phylogenetically by the fusion of more simple parts now regularly develops from a primordium which no longer exhibits the localized polarity necessary for the production of the separate organs. As a rule, however, there is still enough of a tendency toward separation to leave in the compound structure some more or less definite indication of its origin. Such are the notches or longitudinal markings of the gamopetalous corolla, the characteristics employed by the systematist in recognizing the compound ovary, the location of the vascular tissue in discrete strands or fascicles, and various kinds of fluting or bifurcation, as in the style and stigma of maize.

I have been unable to detect in the internal structure of the ear of corn any such evidence of compound structure. The apparent lines of fusion between adjacent rows of pairs of spikelets are really surfaces of contact between the enlarged and hardened bases of the spikelets and do not affect the axis at all. Cross sections of the axis of the central raceme of the staminate inflorescence are lobed in a way which might be regarded as an indication of fusion, but the same conditions are to be noted in sections of the same axis far below the region on which the spikelets are borne, and where probably no one would suggest that fusion had occurred. The vascular bundles are distributed over the section in much the same way as in the vegetative stem except for a tendency toward a peripheral arrangement, which is as pronounced in the four-rowed lateral racemes as in the many-rowed central one.

Other Polystichous Axes in Grasses.—One of the most serious obstacles in the way of this theory is presented by the same type of inflorescence which occurs in other genera of grasses and in which there is no suggestion of origin by fusion. Many complex inflorescences which seem to have their branches arranged in whorls or spirals really have them in distichous groups, each group being a more or less complex system of branches borne on a very short primary branch of the main axis. This is very evident in many species of *Festuca, Poa, Glyceria, Agrostis,* etc., and can frequently be demonstrated in early stages of development of inflorescences which do not show it clearly at maturity. There are, however, many other grass inflorescences in which this distichous, and really dorsiventral, symmetry cannot be detected at any stage of development, and they present a problem of anatomy and phylogeny in no essential way different from that in maize.

Examples of this are found in the large, compact panicles of the grain sorghums, as well as in the more open ones of such species as *Sorghum halepense,* and in the latter it is not uncommon to find radial symmetry in the lower part and distichous symmetry in the upper part of the same inflorescence, a condition comparable with that in some ears of maize. Apparently the same whorled arrangement of branches occurs in many other paniculate inflorescences scattered through the different tribes, but not enough is known about the development of these to enable us to determine in which of them the distichous arrangement has been completely abandoned.

The best expression of this radial symmetry occurs in the genera *Setaria* and *Pennisetum,* and one species of the latter, *P. glaucum* (L.) R.Br., has a fruit which a novice might readily mistake for an unsual ear of maize (Fig. 18, A, C).

The inflorescence of this species consists of a thick axis bearing short branches of somewhat uniform structure, which are arranged in spiral rows. Each primary branch usually bears two fertile spikelets, but it may have only one, or may occasionally have more than two (Fig. 18, B). In maize the two grains borne by the two spikelets of each primary branch regularly stand side by side in a line perpendicular to the length of the ear, and this regularity in number and arrangement causes the grains of the ear to fall into paired longitudinal rows. The irregularity in number and lack of definite orientation of the spikelets borne by one of the branches in *Pennisetum,* however, cause the developing grains to occupy whatever space is available. The result is comparable to that in country gentlemen sweet corn, the fruit showing externally no longitudinal rows (Fig. 18, A).

The real plan of the branching system is best seen in very young inflorescences, while the spikelets are so small that each primary branch appears as a single unit. At this time (Fig. 18, D) the primordia of these branches fall into regular rows, which are soon obliterated externally by the irregular orientation of the developing spikelets. In *Setaria italica* Beauv. the primary branches of the inflorescence elongate and develop into small panicles (Fig. 18, E), which are, however, so uniform in size and structure that they assume a beautiful spiral arrangement or fall into longitudinal rows (Fig. 18, F, G).

Inflorescences of both *Setaria* and *Pennisetum* also occasionally give a fair imitation of the abnormal branching seen in the ear of maize (Fig. 18, H). Such branched inflorescences in *Setaria viridis* (L.) Beauv. are frequently seen where the plants have been damaged by mowing or grazing, and it seems reasonable to attribute this to injury of the growing point at the critical time in the development of the inflorescence. *Pennisetum,* however, sometimes does the same thing without any apparent external cause. Are we to understand that in so doing these inflorescences are reminding us of *their* origin by fusion, as is claimed by some for the branched ears of maize?

No Satisfactory Explanation.—On arranging and evaluating all the available evidences we are forced to the conclusion that all these theories of the origin of the ear fall short of what they attempt to do; and in many respects they add to the difficulty by proceeding too efficiently along wrong lines. Obviously we must look somewhere else for light on the situation.

A Problem of Phyllotaxy

A somewhat different kind of analysis of the situation convinces me that many who have attempted to interpret the ear of maize have been so impressed with the logic of the fusion theory that they have failed to see the obvious. If we first get a clear view of the anatomy of the ear, with all nonessential details omitted, and then a picture of the dynamics of its formation from the growing point of the pistillate shoot, a simple type of mutation is

suggested as the cause of the change from the distichous pattern to the polystichous.

Anatomy of the Ear.—In spite of all that has been said and written about this part of the corn plant, no one has gone very far into the study of its elementary framework. In its earlier stages of development the arrangement of its parts is easily determined, and the ordinary methods of plant anatomy can be applied to its study. Long before maturity, however, the development of a tough sclerenchyma in the peripheral vascular region of the rachis makes it difficult to secure instructive sections even when the technique applicable to

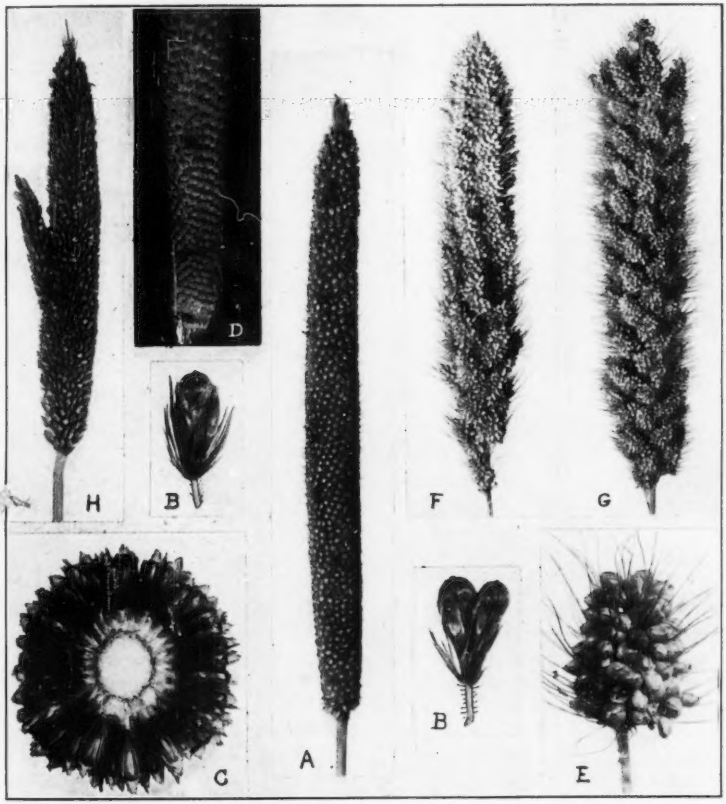

Fig. 18. Inflorescences of *Pennisetum* and *Setaria*. A-D, *Pennisetum glaucum;* B, primary branches; C, transverse section of inflorescence; D, base of very young inflorescence. E-G, *Setaria italica;* F, G, large, well-developed inflorescences; E, primary branch. H, branched inflorescence of *Pennisetum glaucum*.

woody tissues is employed; and, as has been indicated, the information obtained by studying only the external arrangement of the mature grains may be worth less than nothing. Inasmuch as high magnifications are unnecessary, however, it is possible to borrow from the woodworker and the machinist a technique which will yield the desired results.

Good plane sections of matured, dry cobs may be cut in any direction with a fine-toothed saw, and by finishing the surface with sandpaper and varnish much detail can be brought out. One of the most instructive dissections is a cylindrical section made by turning a straight cob in a lathe to remove the chaff and the bases of the spikelets down to the level where the primary branches join the rachis. In the case of crooked or irregular cobs the same results can be secured by first softening the cob by soaking it in water and then shaving off the outer parts with a knife or a small plane.

In cylindrical sections the pairs of spikelets are arranged not only in linear rows but also in certain lateral relationships which seem never to have been considered. For instance, the members of one row are not opposite the members of adjacent rows but alternate with them. Thus, if we count upward from the base of the ear and mark the tenth pair of spikelets in each row, the marked members form an undulating row around the axis, no member being out of line more than halt the distance between two consecutive members of the linear row, and this is as true of the thirtieth or fiftieth pairs in the rows as it is of the tenth. In ears in which the pairs of spikelets are in an odd number of rows, that is, in ears with 10, 14, 18, etc. rows of grains, exact, evenly spaced alternation of every member with its lateral neighbors is, of course, mathematically impossible, but the undulating row around the cob is maintained (Fig. 19, A, B).

If the ear had had its origin by the fusion of racemes side by side, a most remarkable uniformity would have been necessary in the spacing of the primary branches on these to bring about this arrangement.

By plotting the positions of the pairs of spikelets in another way it can be shown that they fall into a system of spirals (Fig. 19, A, B). The regularity of these spirals suggests that we are dealing with nothing more than a complicated problem of phyllotaxy, each pair of spikelets indicating the position of a suppressed axillant bract.

Spiral Phyllotaxy.—The consistent regularity which characterizes the arrangement of leaves in pairs, whorls, spirals, etc. on the stems of various kinds of plants has attracted the attention of botanists for a long time. At least three more or less distinct ways of approach to the problem have been employed in the work of recent times.

With Goethe's theory of metamorphosis as a foundation, Schimper and Braun formulated a century ago the spiral theory of phyllotaxy. The dominant idea was that growth in a stem proceeds in a spiral line, and the arrangement of the lateral outgrowths is an expression of this principle. The fractions expresing the angular divergences between successive members of various types of spirals were found to form a series which had such interesting mathematical possibilities that for a time a kind of philosophical speculation

took precedence over the actual leaf arrangement as the thing of interest; and further progress was possible only when it was recognized that this mathematical principle, as applied to the adult structure, supplied only a part of an explanation.

A later view, supported in one form or another by Hofmeister, Schwendener, Eichler, Schumann, etc., attributed the arrangement of lateral mem-

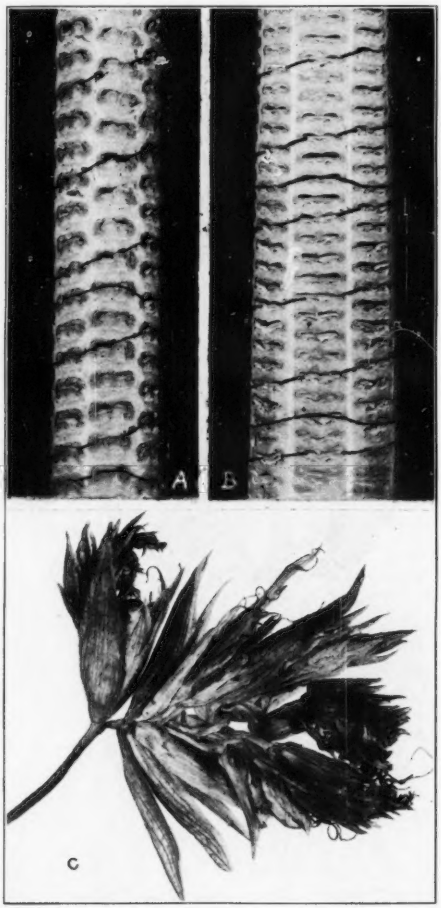

Fig. 19. A, B, cobs with chaff removed and positions of primary branches plotted. C, spikelets in which flower primordia have developed into small ear-like structures.

bers on the stem to the mechanical conditions under which they were formed at the growing point. The climax of this line of attack was probably reached in Schumann's Anschluss theory in 1890.

It was evident that the pressure exerted on the growing point by the leaves covering it was continually being shifted by the origin of new organs. The most favorable position around the growing point for the formation of a new organ was thought to be the place where the pressure was at that time the least.

Church (1904) has modified this theory in the light of the very pertinent observation that, although leaf positions are ordinarily studied on the cylindrical surface of the fully developed stem, these positions are determined by forces acting on the conical, or even almost discoid, surface of the growing point. This conception enabled him to apply certain abstruse geometrical principles to the explanation of all types of phyllotaxy, including some kinds which are too complex to be amenable to other systems.

Application to the Ear of Maize.—A critical examination of the merits of these theories of leaf arrangement is not necessary in applying the principle to the ear of maize. It need only be recognized that the arrangement of the pairs of spikelets in longitudinal series, in spirals, and in regular zonation implies the repeated application of a definite pattern of formation as the growing point moves forward. In certain types of ears these patterns are easily detected, but in others they are less clear.

The two rows of pairs of spikelts of the four-rowed ear, or of the lateral racemes of the staminate inflorescence, exemplify the typical vegetative phyllotaxy of the entire grass family, and the explanation of their arrangement offers no difficulty. They fall along a spiral which passes two leaves in making a circuit of the axis. The angular divergence of 180° between successive members is modified by a tendency toward a type or dorsiventrality which prevails throughout most of the axes of the grass plant.

The eight-rowed ear, whose pairs of spikelets are in four rows, has these members in pairs opposite each other, with successive pairs at right angles to each other. This arrangement may be interpreted as two spirals, each with an angular divergence of 180°. Ears with more than eight rows of grains apparently vary farther from the simple spiral types recognized by Schimper and Braun, but their members still fall in regular spirals and lend themselves readily to explanation on the basis of what takes place at the growing point.

In all of these considerations of phyllotaxy we are reducing observations to generalities in the hope of discovering the pattern which directs the formation of the lateral members in the order in which we find them. The origin of the pattern itself is still as obscure as ever and may never be known.

Whenever the ear of corn has more than four rows of grains, it exhibits a departure from the typical pattern, and an interesting thing about it is that it can do this in different ways, for each new number of rows, as six, eight, ten, etc., represents a different pattern. It follows that somewhere in the phylogeny of the plant a mutation, or series of mutations, gave to it, not

exactly a new pattern, but rather the ability to profit by good physiological conditions and change the pattern. The same explanation will apply to other grasses whose inflorescences show radial symmetry.

That this is true is shown by the readiness with which the number of rows can be changed by modifying the environment. Varieties differ somewhat in the genetic stability of the number of rows, but probably all will respond to extreme conditions affecting nutrition. The most conclusive demonstration of such a change is seen in individual plants bearing two or more ears with different numbers of rows, or even single ears with more rows at one end than at the other, the number of rows in each case being presumably a sort of expression of the condition of nutrition in the plant at the time at which that part of the ear was being formed. There can be no reasonable doubt of the nature of this evolutionary change in phyllotaxy when we see things like this occurring frequently in the development of the individual.

Evidences from Anomalies.—The plausibility of this interpretation is strengthened by at least two kinds of anomalies in which the growing points of the plant develop ear-like structures where they would not ordinarily be expected.

Near the base of the ear or of the tassel there may sometimes be found, associated with the spikelets, small ears enclosed in husks (Figs. 17, F and 20). Dissection of these discloses, in the terminal position, small pistillate inflorescences or fruits, frequently bearing eight or ten rows of grains, but the vegetative structure strongly indicates that the whole organ is a modified spikelet. Each is usually paired with another of its kind or with some structure readily recognized as another spikelet, the outer husks can be identified as the bracts of the spikelet, and an aborted lower flower can frequently be seen in some form. It seems evident here that the primordium ordinarily capable of producing a determinate structure, the two-flowered spikelet, has remained indeterminate, changed its type of phyllotaxy, and produced an ear of normal appearance.[44]

Fig. 20. Small ear which is morphologically a modification of a staminate spikelet.

In another anomaly reported by Fraser (1933) the lower, usually aborted, flower of the pistillate spikelet is often replaced by a small pistillate spike (Fig. 19, C). The morphology of this proliferation as compared with a normal ear has not been fully determined, and there is no indication that it involves any change in phyllotaxy. It does show in a way, however, the ex-

44 Weatherwax (1925).

treme plasticity of the growing point, inasmuch as a primordium having ordinarily the very definite prospect of producing only a single flower, is able to produce at least the semblance of a complex inflorescence in which the flowers are branches of even the third order.

In view of the possibility of such erratic development from primordia in which there is no suggestion of any sort of lateral fusion of parts, why look for any unusual or more complicated explanation of the ordinary pistillate inflorescence or any of its variations?

The Wild Maize Plant

The foregoing description of the various separate parts of the modern maize plant, with the more or less definite evidences as to the course of the evolutionary processes that produced them, permits a degree of speculation as to the nature of the plant at the time at which it was first brought under cultivation by the Indian. Imperfect as much of this picture must be, it may serve as a generalization useful to persons who do not have opportunity to become sufficiently familiar with details to visualize for themselves the plant as a whole and as a guide for anyone who may wish to pursue farther the search for the wild ancestor.

I should expect the wild maize plant to have a tall stem somewhat less branched than that of teosinte, and with a decided tendency for some of the branches to be much better developed than the others. It is highly probable that it was perennial by means of basal offshoots or rhizomes.

Each aerial stem potentially ended in an inflorescence, but there was great diversity in the degree and manner of development of the inflorescences. Those terminating the main stems had a strong tendency to be wholly staminate, while those placed lower on the plant and ending the short branches tended to be pistillate; most inflorescences, however, showed more or less of a mixture of staminate and pistillate spikelets.

Any inflorescence which received a good start in developing was able to maintain this advantage at the expense of those surrounding it. This was associated with two other characteristics, one of which is not encountered in many grasses: the secondary branches on such stems were readily suppressed, and the terminal portions of these well nourished inflorescences responded by changing their pattern of phyllotaxy so that thick axes surrounded by more than two longitudinal rows of lateral members were formed.

The internodes of the branches bearing pistillate inflorescences tended to remain so short that the leaf sheaths overlapped many nodes of the stem above them and usually enclosed the greater part of the inflorescence. The style was elongated and compound, and the pistillate inflorescence quite probably consisted of a somewhat thickened central spike surrounded at its base by a whorl of branches. This general structure of the inflorescence was carried over into that of the mature fruit. Whether each spike had two or four rows of grains we have no way of knowing, because we do not know the history of the de-

velopment of both pistillate spikelets of each pair. In robust specimens the terminal spike of the fruit often had more rows of grains than u :al, and this characteristic soon proved to respond to increased nutrition. The spikes composing the fruit did not disarticulate readily as do those of *Tripsacum* and *Euchlaena*, and the thickened central one did not disarticulate at all.

It seems to me highly improbable that at the beginning of the process of domestication the grains were covered by the bracts as they are in pod corn. The occurrence today of pod ears fully clothed with husks might lead to the conclusion that this was the primitive form of the ordinary ear, and many popular treatises picture this as the type from which the Indian developed the modern varieties. Reasoning in another way, we are tempted to attribute the naked grain, the compound style, and the reduced branching of the pistillate inflorescence to the envelopment of the ear by the husks as the internodes of the axis shortened. We can also find among the *Andropogoneae* ample justification for the hypothesis that in the primitive form the bracts never were as long as they are in pod corn, the unusual condition of the latter being due to some later mutation. In many genera of the *Andropogoneae* all that would be necessary for the production of grains which were almost naked would be the enlargement of the grain so that it would protrude from the ordinary covering of bracts, and the enlargement of the grain was very probably one of the outstanding steps in the natural evolution of the maize plant up to the degree of usefulness which led to its domestication.

I should say, then, that the wild plant had grains which were sufficiently larger than those of other grasses of the locality that they protruded more or less beyond the bracts and were easily removed from the fruiting structure. The reduction of the bracts to their present state as the chaffy covering of the cob probably accompanied the complete sheathing of the ear by the husks; and their hypertrophy to the various conditions seen in different kinds of pod corn probably has no great evolutionary significance.

Along with these more tangible morphological characteristics I would give to this hypothetical wild grass a high degree of mutability. All evidences indicate that the Indian was, for his time and opportunities, a skillful plant breeder, and, by the time of the arrival of Europeans in America, he had made the plant almost what it is today. Its innate genetic plasticity has continued, however, and the modern breeder is carrying on the work.

The wild maize plant of this picture may be disappointing to some because it differs so little, in a qualitative way, from the modern plant. But the differences between cultivated plants and their wild ancestors, where the latter are known, are in general very much of this nature. In the domestication of any plant man has instinctively planted seeds from those individuals which he has liked best, and it is reasonable to assume that these have frequently been the products of abrupt changes. But in such cases there has not been so much the intention of laying a foundation for further improvement as the desire to conserve a stock accidentally discovered. Where conscious selection has been practiced in modern times, advantage has frequently been taken of this rapid method of progress, but much hope of sure success has also been placed in the

slow accumulation of the effects of selection in one direction among minute variations.

I am inclined toward the belief that the most significant difference between wild maize and other grasses, from the standpoint of value to primitive man, was in the size of the grain. A larger grain meant necessarily a grain nearly naked and easily separated from the non-edible parts of the fruit. If teosinte or *Tripsacum* had a grain as large as that of maize, with no increase in the size of the bracts surrounding it, its possibilities as a food plant would be greatly enhanced.

Selection by man has operated on the grain to isolate the various endosperm types and colors but has been chiefly concerned with the increase in size and improvement of shape of what we regard as the normal ear, and this has been done at the expense of all kinds of branches which were in competition with it. This work has been based upon the ability of the ear to modify its anatomy and utilize more than its share of food.

Objection may be raised to this picture of the wild plant because it would be so poorly fitted to live under natural conditions. The seeds possibly had, as they have today, a high viability but low resistance to injury and a poor adaptation to agencies of dispersal. Firmly attached to an axis which did not break into pieces, the grains could either remain on the plant or fall to the ground in a cluster. In either case they would be exposed to decay or to the ravages of animals and insects. If they survived and attempted to grow, the young plants would be so crowded that only a few, or even none, could succeed. Any grain which became loosened from the ear so that it could be acted on by agencies of dispersal would suffer from the lack of protection afforded by the enfolding bracts of other species.

All these characteristics combined certainly do indicate a low rate of reproduction, and we may ask how a plant with such poor adaptations could maintain itself in nature. The answer is that it owes its preservation to its adoption by man at the critical time, and that is why wild maize is rare or extinct today. This is essentially the conclusion reached by DeCandolle early in the history of the sicentific investigation of the question. After a review of the data available to him he says (1884, p. 395):

> Probably so unprotected a species was becoming more and more rare in some limited region, and was on the point of becoming extinct, when a wandering tribe of savages, having perceived its nutritious qualities, saved it from destruction by cultivating it.

This matter of the extinction of a species has many interesting aspects. We can easily proceed too far on the theory that every characteristic of an organism plays a useful part in its fight for life. It is necessary that we recognize that many characteristics are detrimental, and many others are at least useless. Success of the species demands hardly more than a favorable balance of the good over the bad under the prevailing conditions. The geologic record, moreover, is full of instances in which species have, for no known reason, developed useless or detrimental features to the extent that with only slight environmental changes, or even no change at all, the balance has become unfavorable and extinction has resulted.

But, after the species is doomed, it is not necessarily snapped out of existence instantly. Its fight may extend over centuries, marked by many gains and relapses, and an observer may not in a lifetime be able to detect any appreciable progress.

If the chief defects of the plant under consideration were in its method of seed dispersal and its mechanism of dormancy, as has been postulated for maize, and if the plant were also able to propagate by means of some perennial vegetative structure, the time required for extinction might be greatly extended. On the other hand, the process might be greatly accelerated by some significant environmental change. The introduction of grazing livestock into America early in the sixteenth century may have had just this effect, as grazing has operated on *Tripsacum dactyloides* in some localities in the southern part of the United States.

In view of these conditions I think it not wholly improbable that in some isolated, well protected locality in tropical America the wild maize plant may still be growing. Great areas of the highland region of Central America and southern Mexico have never been visited by explorers competent to recognize such a plant if they found it, and in such a rich flora it might easily be overlooked. There are plenty of places protected from grazing animals by thorny vegetation and other obstacles in which the plant may still be fighting its losing battle. Because of this possibility, every plausible report that may have any bearing on the question should be thoroughly investigated.

How Many Species?

Linnaeus gave to the corn plant the technical name *Zea Mays*,[45] although both parts of the name had previously been applied in a less systematic way. He probably had no idea of the great variability of the plant, or he may have been inclined to treat cultivated plants in broad terms; otherwise it is difficult to see how, with the point of view of his time, he was satisfied to make this a monotypic genus.

As the variability of the plant became better known in later years it was observed that many agricultural varieties or sporadic characteristics were not included in Linnaeus' conception of the species; and new names were created to designate these new taxonomic concepts.

Many of these names suggest the characteristics which, in the judgment of their authors, required recognition. The following are examples: *Zea cryptosperma* Bonaf., *Z. altissima* Gmel., *Z. hirta* Bonaf., *Z. alba* Mill., *Z. macrosperma* Klotsch., *Z. rostrata* Bonaf., *Z. minor* Gmel., *Z. ramosa* Gernert, *Z. tunicata* Sturt., etc.

45 The capitalization of the word *Mays* in this name has sometimes been questioned or criticised. Those familiar with the history of botanical nomenclature recognize this as one of those instances in which a word once used in a generic sense now designates a species. *Mays* is a proper noun, an old generic name, here used in apposition with the word *Zea*, and many botanists prefer to retain the capitalization for the sake of its historical value. Although others may choose to decapitalize all specific names, capitalization in cases like this has by no means been abandoned to the extent that it represents bad usage.

One system of classification employs the chemical and physical nature of the endosperm as the distinguishing characteristic and gives technical names to the main agricultural varieties on this basis. Sturtevant's classification (1894, 1899) is probably the best known. He regards pod corn (*Zea tunicata* Sturt.) as the primitive, cosmopolitan type and names the agricultural derivatives as follows: pop corn, *Zea everta,* dent corn, *Z. indentata,* soft corn, *Z. amylacea,* flint corn, *Z. indurata,* and sweet corn, *Z. saccharata.* Other authorities, choosing to regard these subdivisions as varieties, rather than species, have listed the series as *Zea Mays tunicata, Z. M. everta,* etc.

A complete list of all the technical names that have been applied to the different kinds of maize would doubtless run well into the hundreds, and the names become as complicated as the things which they attempt to name. The futility of treating the varieties in this way is well demonstrated by the fact that none of these names are generally used, and those that are employed to any extent are used to designate individual characteristics, or groups of closely related characteristics, rather than true taxonomic units. It is to be noted, too, that even according to Sturtevant's classification a single individual might belong to two or more species at the same time. An ear of dent corn may have the grains podded, in which case it would be simultaneously *Zea tunicata* and and *Zea indentata.*

To find a remedy we may well ask what is expected of taxonomy in a situation like this. If a species or variety is to be regarded as only an abstract concept, that is, only a convenient receptacle, determined by a description and a type specimen, this system probably fills the requirements. But workers in other fields have a right to expect more than this of taxonomy.

The subdivisions of the genus which have been named have been based on the *prominence* of certain characteristics rather than on a *consistent correlation* of characteristics, and the mention of a name conveys no impression of the plant except with respect to this one characteristic. For example, the name *Zea saccharata,* applied to the various sweet corns, tells nothing except that there are certain limitations on the ability of the endosperm to convert its carbohydrate into starch. In stature, length of growing season, structure of inflorescence, degree of suppression of vestigial organs, etc., it may represent practically the whole range of variations exhibited by the genus. In fact, genetic experiments have shown that if we give to any ordinary variety of sweet corn the full ability to build starch grains, it may readily differentiate into dent, flint, and soft varieties. It is doubtful whether taxonomic nomenclature should be asked to invent names for such variations, and, if it does choose to assume this responsibility, the names mean so little that no one is much concerned about remembering them.

The fundamental function of taxonomy is to recognize at the present time the diverse units which evolution has produced and place them in order. The best test of the unity of a group is the occurrence in all its members of a set of characteristics which have no reason for being associated except that the organisms that have them have had a common history; and the best reason for excluding an individual, or group of individuals, from such a unit is the

lack of this correlation of unrelated characteristics. The named varieties and subspecies of maize fall short in just this respect.

It is highly probable that there was a time when the ancestry of all the maize plants now in existence consisted of only one or a very few individuals which had diverged from some other stock. If we had been dealing with the plant at that time there would have been little difficulty in disposing of it taxonomically; and, if natural processes had been allowed to take their course, the taxonomic problem would probably never have become very complicated. Granting a high degree of mutability, we may still assume that the rigors of natural environment would have destroyed most of the innovations; and what was left would have constituted a single more or less heterogenous collection of individuals which might properly have been called a species.

If this species were vigorous, and if extensive migration had occurred or effective barriers had been interposed in its habitat in some other way, the stock might have separated into two or more species. The situation would then have been somewhat comparable to that which we have in such a genus as *Tripsacum*. But it was probably not a vigorous stock, and only the intervention of man saved it from extinction. This incident also diverted the course of evolution by doing two things which nature ordinarily does not do. Man preserved many characteristics which had a low, or even negative survival value; and, by exchange with his neighbors, he neutralized any effect that natural barriers might have had. We see the result today in a complex of intergrading varieties, none having any constant, exact identity, and none constituting independent ultimate branches of the genealogical tree. If we describe and name such units, the names and descriptions mean little or nothing.

The taxonomist's only satisfactory recourse is to treat the whole complex as a single species, because that is the smallest unit that can be separated from anything else. This could be represented diagrammatically, not by a single twig or fascicle of branches of the genealogical tree, but by a complex unit whose branches are tied together in all kinds of ways by a system of anastomoses and cross connections, with no free ends. This is the unit which may appropriately be named, and which we may regard as having been named by Linnaeus, even though he did not know fully what he was naming.

The best procedure seems to be to regard *Zea* as a monotypic genus and to designate agricultural varieties by means of common names. When special characteristics are under consideration they can be cited directly and described briefly inasmuch as they are not consistently associated with other characteristics. This is essentially the procedure that is generally followed today.

Maize and Teosinte

Our picture of the wild maize plant cannot be regarded as complete, even in a hypothetical way, until it takes into full consideration the genus *Euchlaena* and is at least consistent with what we know about *Tripsacum*. The remarkable similarity between maize and teosinte, their genetic compatibility, and their apparently overlapping distribution indicate that they have shared

the same heritage and at least similar surroundings in the past and have yet in some way maintained a high degree of phylogenetic individuality. It is in the interpretation of the relationship of these two genera that we find one of the main differences in recent theories of the origin of maize.

Teosinte was first introduced to the scientific world through mention of it in a seed list in 1832, and its relationship to maize and *Tripsacum* was first seriously considered about 1876. At that time *Zea* and *Euchlaena* were regarded as very near relatives, the latter even being mentioned as a kind of *Zea* with a pistillate inflorescence like that of *Tripsacum*.

As a natural consequence of the similarity of the two plants it has frequently been suggested that teosinte is merely the wild form of maize. This view is readily accepted by many who have seen both plants but have never examined closely the evidences of their relationship. It is reflected in the statements of many students of archeology who say that the ancient American races produced maize by domesticating teosinte.[46] Many statements even go farther and say that the Indians produced the *three principal varieties* of corn by domesticating *three wild grasses*.[47] Harshberger for a time gave this idea favorable consideration after he had discovered that the plant which he had previously regarded as wild corn was a hybrid between corn and teosinte.

Conclusive evidence of this relationship would be afforded by an experiment in which, starting with teosinte and selecting with that definite end in view, we should accomplish the production of something closely resembling corn. Two such demonstrations have been reported, one by Luther Burbank[48] and the other by Blaringhem (1924) in commenting on the work of Bento de Toledo. In both instances, however, if we are to trust the published pictures, the material which provided the starting point for the experiments was a hybrid between corn and teosinte. They make no mention of the purity of their stock or of the means employed to prevent contamination with corn pollen while the experiments were in progress. The sum of these shortcomings is suffiicent to render these reports valueless as evidence on the ancestry of maize.[49]

The principal objection that has been raised to our considering teosinte as the wild form of maize is in the nature of the specialization of the two plants. Both are highly specialized, but in different ways. Maize has the generally reduced vegetative structure, which is apparently correlated with the thickened axis of the pistillate inflorescence. Teosinte has the hardened, articulated rachis and outer glume forming a covering for the seed. Each genus is, in some ways, more highly specialized than the other, and to have

46 Gann and Thompson (1931, pp. 9-10).

47 Thompson (1932, p. 22).

48 This idea runs through several of the popular articles attributed to Burbank. The results of this experiment were first published in the magazine section of a Sunday newspaper and then copied in the Literary Digest for July 9, 1921.

49 For critical analyses of these reports see Weatherwax (1925) and Collins (1925).

either derived from the other would imply regressive changes which seem improbable.

Under human direction this sort of change might be possible, but it would be difficult to imagine what the primitive man's motive would be in giving such direction. The young shoots and inflorescences of teosinte and *Tripsacum* are said to be used for food in some localities, but evolution toward the maize type would probably not improve their qualities in that respect; no more would the plant's forage qualities be improved by such breeding, even if the ancient American races had had any use for forage plants; and the small grains of teosinte, enclosed in their indurated covering, would have offered so little reward to the primitive farmer that he would have taken no interest in either breeding or cultivating the plant.

It should be noted, however, that, with all its limitations as a promising agricultural plant in ancient America, teosinte was within one short step of being a most useful plant, and that step could conceivably have been accomplished by a single mutation. Any change which would have increased the size of the grain, especially the endosperm, so that it would protrude beyond its normal bony covering, would have made it a better cereal than any other grass known in America at that time if there were no maize.[50] The general plasticity of the endosperm of maize, as indicated by what breeding has done for it, strengthens the plausibility of such an idea. Such a plant would, however, lack one other important characteristic of maize, namely, the ability to concentrate its resources into the production of relatively few large fruits. The Indian, having been attracted by the large-grained form of the plant, and having found that it responded well to his efforts, might have taken advantage of later mutations to begin the course of selection which resulted in the maize plant of today. The degeneracy of the glumes and the loss of induration would still be unexplained.

It seem to me much more in accord with our general ideas of evolution to picture the forerunner of maize as having separated much earlier from the same stock as the *Andropogonae* and having pursued its own course of evolution in complete isolation from teosinte, arriving ultimately at the combination of characteristics previously listed in our description of the hypothetical wild plant at the time of its adoption by the Indians.

Whatever may have been the place and manner of origin of maize and teosinte, they have now long grown in the same areas in tropical America, frequently with the plants of both mingled in the same community. Since the two freely hybridize, we next ask how they have maintained their separate identities.

The two plants wherever they occur are ordinarily distinct. Either may be slightly contaminated with the other, teosinte especially showing some traces of the maize character, and other plants which are certainly hybrids between

50 One or two wild species of *Oryza* in tropical America might have offered suitable material for domestication, but their usefulness was limited by their need of a semi-aquatic habitat.

the two are encountered; but there is no finely graded series of forms between them. The collector, knowing that the plants hybridize, seldom has difficulty in identifying any particular specimen as belonging to one species or the other or as a recently produced hybrid.

This would indicate that, although the hybrids are fertile among themselves and with either parent, they do not, for some reason, have as good an opportunity to survive as do the parent forms. I attribute this to two selective factors which have been present since the ranges of the two species were first made to overlap. One of these is man. He has for a long time had a pretty definite idea as to the kind of corn that he desired, and he has known in a general way how to get it by seed selection. Many teosinte characters have been objectionable in a cereal, and he has rejected them. Nature has provided the other selective influence. Many of the maize characteristics expressed in the hybrids are low in survival value. Among these may be mentioned the large, many-seeded, unarticulated fruit and the naked grain; and plants having these characteristics have had little opportunity to leave offspring. Thus man has, on the one hand, tended to perpetuate maize, and nature has, on the other hand, selected toward teosinte. The hybrids, although continually coming into existence, have been favored by neither selective influence and have usually failed to make any progress toward bridging the gap between the species.

Theory of Hybrid Origin

An entirely different relationship between maize and teosinte has been pictured in another theory which has stimulated much discussion in recent years. According to this view, the maize plant originated through the hybridization of teosinte with some other grass which has only a hypothetical existence.

History.—This theory was first expounded by Harshberger in 1896. He had previously made an intensive study (1893) of the biological nature and agricultural utilization of maize, basing a prominent part of his work on a plant which he supposed to be a wild variety, but which turned out to be a hybrid between maize and teosinte.[51] In a new consideration of the question after the discovery of this error he virtually abandoned the idea that maize had arisen as an independent species and favored the theory that it arose through hybridization of teosinte with some other plant. This other plant was pictured as either some grass of unknown identity or some variety of teosinte itself which had been improved by cultivation. Ultimately he regarded the latter as the more satisfactory explanation.

A few years later Collins (1912) reviewed the subject and gave his support to Harshberger's theory that maize arose as a cross between teosinte and some unknown grass, picturing the latter as some member of the *Andropogoneae* which had many of the characteristics commonly seen today in pod corn.

In a review of the question in 1918 the writer described in detail the inflorescences of *Zea*, *Euchlaena*, and *Tripsacum* and concluded that the

51 See p. 58.

facts did not require any more complicated or less direct explanation that that the three genera had arisen from some common ancestral stock by the ordinary operation of mutation and selection. This thesis was immediately attacked by Kempton (1919), and since then he and Collins have published a number of articles restating some of the old arguments and presenting some new ones.

The following is probably a fair summary of their arguments:

1. The numerous points of anatomical and physiological similarity between maize and teosinte, and their almost complete interfertility, indicate a closer relationship than would be expected if they had remained independent of each other long enough to develop the differences which separate them.

2. The genetic complexity of maize, as shown by its high degree of heterozygosity, the frequency of its mutations, many of which result in monstrosities, and its cytological irregularities, suggests a hybrid origin.

3. The well known intolerance of maize to self-fertilization is attributed to the peculiarity of the unknown parent which hybridized with teosinte.

4. The series of forms produced when maize is hybridized with teosinte suggests a back cross between a hybrid and one of its parents rather than a cross between two stocks separated by differences that may be attributed to gene mutations.

5. The time during which, by most liberal estimates, man has been in America is too short for him to have made by ordinary methods of breeding the changes that have been made in maize since it was a self-supporting wild plant, and hybridibation is invoked to account for the speed of the process.

Some of these points have, I believe, been misinterpreted or given values out of proportion to their significance; and some have had the misfortune of being cited in support of a theory in the original formation of which they had no part.

Heterozygosity of Maize.—Practically any variety of maize which has not been scientificially inbred is highly heterozygous, and this condition is, of course, a good indication of hybridism. I see, however, no indication that anything contributed to this hybrid condition but the different varieties of maize itself. The plant is in a very plastic condition as far as mutation is concerned, and isolation with some sort of selection would undoubtedly have produced long before this many separate stocks which could be regarded as species. Such barriers as have been present in the maize area during the period of its agricultural exploitation have, however, been insufficient to prevent intercrossing, and such variants as have had the potentiality of becoming separate species have been always losing themselves by back-crossing with the parent stock. The varieties that we have today are, therefore, essentially like interspecific hybrids in nature, but we need not look beyond the genus *Zea* for the materials of their ancestry.

That a hetreozygous stock like this should give a *series* of forms when crossed with a comparatively homozygous stock like teosinte is in accord with what would be expected. The back-crossing of any hybrid with one of its

parents gives a series of forms, not necessarily because they have three-fourths of their ancestry from one source, but because a heterogenous stock is being crossed with a comparatively homogenous one.

Response to Self-fertilization.—The difference between maize and teosinte in their response to self-fertilization is so naturally correlated with certain other conditions, and so well illustrated among other organisms, that it calls for no more than a general explanation.

Under ordinary field conditions in the regions where corn is grown today the plant is more than 90% cross-pollenized, and the agricultural practice of the Indians during the long period in which the plant was undergoing a significant part of its evolution was such as to insure almost complete cross-pollination. Since they had no draft animals and only very primitive implements, the preparation of a field before planting corn was a heavy task. They usually met the situation by first planting the crop and then pulverizing the soil and heaping it around the plants as they grew. It suited these limitations of equipment, and often the Indian's temperament as well, to do as little of this work as possible, and several grains were planted in each of the rather widely spaced hills.

This method, as far as significant details are concerned, seems to have been practiced throughout the corn-growing regions of ancient America; and, with the substitution of the metal hoe for a clam shell, or the machete for a sharpened stick, it is still extensively employed by the Indians in many places. As a rule today, where this primitive method is used and corn is planted year after year in the same fields, the planting is done in the spaces between the hills of last year, and cultivation tears down the old hills and builds new ones. In some sections, however, the same hills were used year after year, being built higher and higher with successive cultivations; and in some places the quickly encroaching grasses have preserved in the sod these beds and ridges of cornfields abandoned centuries ago.

The arrangement of the inflorescences of maize and the general occurrence of protandry make it obvious that any individual's opportunity for self-pollination is greatest when it stands as far removed as possible from any other individual. When two or more plants are grown in close proximity, the individual's chance of receiving its first pollen from some other member of the group is very great, and this chance is greatly increased by the fact that the maximum release of pollen and the maximum receptivity of the stigmas seldom coincide in the individual plant.

The close proximity of the plants in a hill discourages the production of tillers and has undoubtedly exerted a selective influence by placing a premium on any genetic tendency to suppress them. Conscious selection has also tended to eliminate tillers and superfluous pistillate branches. The effect of all this has been to reduce the number of inflorescences of any one genotype and consequently to reduce the chances for self-pollination.

In teosinte the situation is entirely different. A single seedling may branch at the base to produce a large number of culms, each of which behaves like an individual plant, and the profuse branching of the culms may result in the

production of hundreds of inflorescences of both sexes from a single seed. The influence of cultivation, so significant in the case of maize, has been lacking, and the plant has probably always experienced a high degree of self-pollination.

The order of flowering in the staminate and pistillate inflorescences is the same in both species, and in androgynous inflorescences, which occur commonly in *Zea* and more rarely in *Euchlaena*, the pistils regularly mature before the stamens at any one level. In the conditions connected with flowering there is no difference between the two which cannot most logically be attributed to these effects of cultivation, and I can see no occasion for looking for any mythical ancestor which might have brought protogyny into the heritage of maize.

Teosinte, being self-pollenized, has always been inbred, is highly homozygous, and is genetically adjusted to inbreeding. Maize, on the other hand, has been largely cross-pollenized for a long period, and the part of its genetic composition which remains with us is highly heterozygous and shows a marked response to a change in the type of reproduction to which it has become adjusted.

Mutation and Monstrosities.—Before we can seriously consider the frequency of mutation or the production of monstrosities as even suggestions of hybridism we must know more about the cause of mutation. This question has been raised in connection with the behavior of other mutable stocks, and I am not aware of any clearly defined evidence that hybridism is ever the cause of a real mutation. Even if such a principle were firmly established, we should here be confronted with the difficulty of distinguishing between the theoretical hybridization which brought together the characters of the genus and the very real hybridization which has been going on for ages among the varieties of maize itself.

Date of Domestication.—Evidences previously cited indicate that the period which has necessarily elapsed since the first domestication of maize has been greatly over-estimated by the proponents of the theory of hybrid origin. Using as a measure the progress that has been made in the evolution of maize within the period about which we have reasonably definite information, Collins (1931, p. 207) believes that "assuming anything like a uniform rate of change" more than 20,000 years would have been necessary. But a careful weighing of the evidence afforded by what he regards as fossil remains materially reduces the period about which we have definite information; and the assumption of anything like a uniform rate of change seems entirely erroneous. The most striking and fundamental changes resulting from intelligent selection would probably come within a few years after the beginning of domestication, and the curve of progress would soon flatten. It is evident also that in order to accept the independent evolution of the plant Collins would demand more difference than is really necessary between modern maize and its self-supporting ancestor, and a longer separation than is evident between maize and teosinte. In the latter connection he implies (1931, p. 209) that the two species would have been separated since "they originally diverged from some

perfect-flowered form," a supposed situation which is as absurd as it is unnecessary.

Plausibility of the Theory.—All will agree that there was somewhere in the ancestry of maize a kind of plant which is now extinct or at least unknown. The question on which we differ is whether this prototype gave rise to maize by direct evolution, probably guided by man, or whether it first hybridized with teosinte. Those who regard with skepticism the latter idea do not see in maize any very great indication of this hybridization and do not see any theoretical need of it.

The unknown parent which could have hybridized with teosinte and produced maize, but which could not have produced it by direct evolution, presents probably the greatest difficulty. None of its varied characters presented in the different discussions are very satisfactory. Harshberger's idea that it was a cultivated form of teosinte itself has been abandoned because of the improbability that teosinte would be cultivated in the first place. The nearest that anyone has come to any other picture of it is in Collin's first discussion (1912) of the question, where he attributed to it many of the characteristics of pod corn. To say that it was a member of the *Andropogoneae* is very indefinite in view of the fact that that tribe is large and heterogenous. To find a plant near enough to teosinte to permit hybridization, and yet lacking in the fundamental essentials for the origin of maize, seems practically impossible. In other words, if we must go into the realm of theory for the plant's ancestry, it will be as easy to find all of it there as half of it.

There is also some question as to the exact nature of the alleged hybridization. Did our maize plant, in all its range of forms, come from a gradual mass blending of two species or races whose habitats came to overlap? Or, did it originate from a single fortuitous hybridization which produced one or a few promising individuals at the right time? It would seem that we were justified in requiring somewhat definite answers to these questions before abandoning a simple, direct theory, which is as satisfactory as can reasonably be asked, in favor of one encumbered with all the inconsistencies and uncertainties connected with that of hybrid origin.

Place of Origin of Maize

At the time of the early exploration of America by Europeans maize was so widely distributed and there had been such a free exchange of many of the varieties among the different races of the aborigines that it would have been impossible even then to map with any certainty the lines by which the plant had radiated out from its original home. Since then the routes of migration of the ancient races and their cultivated plants have been so thoroughly erased that little evidence is left as to where maize had its origin, except that it was somewhere in America.[52]

The botanical character of the plant strongly suggests that its natural home was in a tropical or sub-tropical upland region, away from the competition of

52 Merrill (1930, 1933); Cook (1925).

the jungle and the rigors of a long cold season; and this eliminates from consideration the greater part of both continents. It leaves, however, two very favorable places, central Mexico and Peru, which have received most consideration, chiefly because they have been the seats of the series of civilizations culminating in the Aztec and the Inca of the time of the conquest. As the mystries of the Mayan culture yield to the attack of the archeologist and the ethnologist, a third claim for credit must be considered.

South America.—The claims of northern South America are best supported by the somewhat indefinite reports of peculiar varieties of corn in Paraguay, to which reference has already been made,[53] by the great diversity in cultivated varieties of maize and other plants in Peru and Bolivia,[54] and by the elaborate uses of maize in the Inca arts and industries.

Mexico.—The Mexican plateau also supported a high civilization correlated with corn in many ways; a large number of varieties were grown; and we have at least Boturini's report,[55] of a wild variety of corn growing in the nearby lowlands. But probably the best evidence is provided by the spontaneous occurrence there of teosinte.

The Maya Area.—It has seemed to some less likely that the Mayas were the first to domesticate maize, because the climax of their civilization was reached in the jungle regions and in Yucatan, neither of which could well have been the home of wild maize. It will be remembered, however, that the Mayan culture of which we hear most was comparatively recent, and in their earlier migrations the forerunners of this race were well acquainted with the highland regions where the wild plant might have grown. They have at least two outstanding traditions which tell of their receiving maize and being taught the rudiments of agriculture.[56] These might indicate that a practice was borrowed from a neighboring tribe or that agriculture was introduced by the incorporation of other tribes into their empire. There is much uncertainty as to the identity and relationships of the forerunners of the Mayas and the Aztecs, and they seem to have had much in common. Since their territories were contiguous or frequently overlapped, we need not consider seriously a distinction between the two as far as the *place* of the origin of maize was concerned.

Vavilov's Principle.—There is still some difference of opinion as to which of the two regions, Peru or the Mexican highland, has the better claim as the place of domestication of maize. Cook (1925) believes that Peru was the outstanding general center of domestication of plants in ancient America and probably the seat of one of the oldest systems of agriculture in the world, but he grants that a long time before the Spanish conquest there had been an interchange of culture with Mexico and the West Indies. This leaves open the possibility that maize was an exotic in Peru.

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53 See p. 6.
54 Cook (1925).
55 Schellhas (1929); Nuttall (1930).
56 See p. 4; also Sturtevant (1919, p. 608).

As a result of extensive study of the cultivated plants of the Eastern Hemisphere, Vavilov has devised the general formula that "the home of a cultivated plant is —— the region where the primary varietal potential of the given plant is concentrated."[57] If this principle were applied to the maize problem, Collins (1931, pp. 202-203) concludes that the Andean region would be indicated as the center of domestication because it shows a greater diversity of types than all of North America. Vavilov applies the same formula to the problem, however, and gets a different result (1931, pp. 195-198). Because of the effects of irrigation he discounts the great variability of maize in Peru and holds that the "great varietal potential" and "great ecological variation" in southern Mexico and Central America are of more significance and indicate the origin of maize there.

The attitude of most botanists will probably be one of conservative skepticism until Vavilov's method has been shown to be as efficient as he apparently believes it to be. Granting that it has the sound backing of extensive field observation and that it is consistent with the data on the small cereals of Europe, we may still question whether it can be applied as a formula in determining the distribution of other cultivated plants in general, particularly when the latter embody as many unique characteristics as does maize.

Range of Teosinte.—Probably the best single indication as to the place of origin of maize is afforded by what we know of the natural distribution of teosinte. The annual form of the latter is a common weed in cultivated fields in many places on the Mexican plateau and has been taken to other parts of the world for use as a forage plant.

Except for one early report of its occurrence in Guatemala,[58] it was for a long time not known in anything like the wild condition outside of Mexico. In December, 1931, however, Dr. Wilson Popenoe, of Guatemala City, investigating a report of its occurrence near the frontier of Salvador, found the plant in several places near Jutiapa.[59] I visited this locality in March, 1932, and, although it was during the dry season and the plants were dead I was able to get a good idea of the conditions under which it grows.

The dead plants and mature seeds indicate that the variety is much like that grown in Florida. It grows in cornfields in several places but evidently flowers so much later than corn that hybridization is not common. Hundreds of individual plants with friuts still enclosed in the leaf sheaths were examined, but not one showed the ordinary indications of hybridization.

As in other places, the local name is "maycillo" or "teosinte." No one

57 Vavilov (1932, p. 82). The same principle is stated in an earlier paper (1929), but the quotation gives it in the most clear and concise form.

58 Seeds of a plant called Téozinté were sent to France by J. Rossignon, director of the Botanical Garden at Guatemala City, in 1869. See Bull. Soc. Imp. Zool. Acclim. II. 6:487-488. 1869.

59 Reported by Collins (1932). There is little doubt that the seeds which Rossignon secured were from the same locality, and it is possible, at least, that the variety now grown in Florida, which is said to have come from France, was from this source.

seemed to be particularly interested in the plant except to say that it sometimes provides food for cattle. One boy told me that the seeds are sometimes fed to poultry, but he was evidently overimpressed with my desire for information and may have invented a use for it to please me.

The plant undoubtedly grows wild in this locality. Although it seems to thrive best in poorly cultivated fields along with corn and other crops, this seems to be because it finds there better soil and less competition and is protected from grazing animals. The situation seems to be much the same as that for some of our common weed grasses such as *Setaria lutescens*, which finds one of its best habitats in fields with annual crops, or *Bromus secalinus*, which is very much at home with winter wheat. It is evident, too, that teosinte is persisting there also outside of cultivated areas. In several places it has spread over rocky hillsides which have certainly never been cultivated, and for most of the six miles along the road between Jutiapa and Progreso isolated specimens or small colonies of the plant can be seen along fence rows, among thorny shrubs, or in other places protected from livestock.

At the Torlon mine, near Huehuetenango, I learned from Indians of a plant which was said to be common in a locality near Kamoña, several miles to the northwest, near the Mexican boundary. Indians hired to visit the place brought back seeds, seedlings, and dead stems of teosinte.[60] Other clues received from the Indians proved to be of no value. Particularly interesting were certain reports of plants known as "madre de mais," but "mother of maize" seems to mean to them some plant that can be used as a substitute for maize rather than the phylogenetic ancestor of the plant.

Later I learned from a missionary at Huehuetenango of another locality, near San Miguel, where a similar plant is said to cover the mountains. The description, given without prompting on my part, is evidently that of teosinte.

These extensions of the range of teosinte, even to the one at Jutiapa, do not, I believe, add materially to the significant information that we have on the corn problem, because the plant was already known from the adjacent parts of Mexico, and the restless movements of the Indians, individually and in large groups, which have taken place for centuries could easily have spread the plant, particularly if they had had any real or imaginary use for it. This new information will, however, provide material for any who may see significance in the occurrence of teosinte in the Maya region.

Necessity of Isolation.—Granting that the nearest known relative of maize is teosinte, and knowing fairly well the natural range of the latter, we might at first think that the home of wild maize should be sought in the same area. If, however, *Zea* and *Euchlaena* arose by ordinary divergent evolution from a common ancestral stock, there must have been some sort of barrier between them, enabling them to retain their independence of each other over the long period while they were developing the differences which separate them today. There was apparently no genetic incompatibility, structural peculiarity, or significant difference in time of flowering to which this could be attributed, for

60 I am greatly indebted to Mr. Louis Leysbeth, operator of the Torlon mine, for help in securing this and other information from the Indians.

the two are known to hybridize freely where they grow in the same habitat. From this it may be concluded that the two plants ran their respective courses in complete isolation from each other, separated either by distance or by some physiographic feature.

If separated by a natural barrier they might have maintained their genetic independence in the same general region, and the diversified topography of the plateau region of Mexico and Central America offers abundant possibilities. The innumerable steep-sided, narrow ravines, sloping down from the high plateau to the jungle, offered an ideal habitat for either plant with almost complete isolation, at least until man became an influential factor. The likelihood of either plant's being carried over the mountain barrier by birds or animals would have been slight, and migration over the barren ridges, step by step, would have been almost impossible. The easiest direction of migration would have been down the valley, but escape there was blocked by the jungle, as effective as the sea in preventing the spread of such a plant as maize or teosinte.

It need not, however, be inferred, and I believe it is hardly probable, that both plants developed in such limited habitats as the one described. In view of its relatively better adaptation to life under natural conditions and its lack of correlation with man's activities, I believe that the distribution of teosinte, as determined since its discovery a hundred years ago, represents its natural distribution much better than the map of maize at the beginning of the sixteenth century represents the natural distribution of this species before it was adopted by man.

Effects of Domestication.—We may conclude, I believe, that at some remote time teosinte was rather widely distributed, where soil, altitude, and climate were suitable, over the highlands and foothills of central Mexico and western Guatemala, while maize, handicapped by its bizarre specializations, was fighting a losing battle in some isolated place. Then man, with his capacity for civilization, came on the scene as a new and profoundly significant factor of environment; and a group of characteristics which would soon have spelled the doom of the species under natural conditions suddenly assumed great survival value, rose above all biologic and physiographic barriers, and started the migration of the plant into every part of every continent where any sort of suitable environment existed.

Teosinte, in the meantime, held its place until the coming of Europeans at the close of the fifteenth century. Then a new factor influencing its welfare came in the form of large grazing animals, and teosinte was compelled to retreat to protected waste places or to seek protection as a weed in cultivated fields.

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BALD CYPRESS, TAXODIUM DISTICHUM (L.) RICH., AT HOVEY LAKE, POSEY COUNTY, INDIANA

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Some especial interest is attached to the bald cypress in Indiana because of its conspicuous rôle in that rather small group of extraneous, southern-lowland plants which are found in the botanical-physiographic region known as "The Lower Wabash Valley." Some other woody species of this group beside *Taxodium distichum* are *Carya Pecan, Quercus lyrata, Q. Shumardii, Q. rubra* var. *pagodaefolia, Gleditsia texana, G. aquatica, Acer rubrum* var. *Drummondii, Catalpa speciosa, Forestiera (Adelia) acuminata, Ilex decidua, Vitis rubra, Aristolochia tomentosa,* etc. The nomenclature used and the distributional data are those of Deam's "Trees of Indiana" (1932) and "Shrubs of Indiana" (1932). Botanists in general have been interested in the bald cypress (and its close relative, *T. ascendens* Brongn.) for its production of pneumatophores, or knees, and its buttressed condition. Recent papers of interest include Kurz (1930), Welch (1932), Demaree (1933), and Kurz and Demaree (1934), which describe some of the conditions for, and types of buttress formation, knee formation, and germination and establishment.

The Indiana stations for *Taxodium* are of interest because they represent northern outposts of the species in the Mississippi Valley section of its distribution. Deam remarks, "The present indications are that the cypress will be extinct in Indiana before many years because practically no small trees can be found." Welch (1932) remarks that in a small cypress swamp east of Mt. Vernon, Indiana there were thousands of first year seedlings and hundreds of saplings up to 8 feet high but that there was a large gap in size between this group and small trees 1 foot in circumference. There was an abundance of trees larger than 2 feet in circumference. Collett (1874) and Wright (1898) discuss the cypress in Indiana in the days before its decimation, when thousands of acres of virgin cypress forest still existed. No cypress remains in most of the areas they described.

The author, visiting one of the few remaining sites of cypress in Indiana at Hovey Lake, noticed the general absence of cypress reproduction and knee development in stands where mature trees are now dominant. In 1932 an effort was made to obtain statistical data on the cypress woods and to gain more accurate information concerning the quantity of reproduction.

Hovey Lake, not far from the junction of the Ohio River and the Wabash River, occupies an old river channel in southwestern Posey County, Indiana. The lake lies about 8 miles south and a little west of Mt. Vernon, the county-seat. The lake is shallow and has a mud bottom. The west bank rises abruptly twenty to thirty feet from a narrow terrace. On the other sides the lake margin merges gradually into the general floodplain of the region. Mostly the timber has been cut from the region but there is a wooded border to the entire lake although rather narrow in places. To the south and east there are

some low marginal areas with a considerable acreage of forest. Hovey Lake is well-known to fishermen and hunters. There have been several papers dealing with the ornithology of the region for certain austro-riparian species are more common there than anywhere else in Indiana.

About 4 miles of Hovey Lake, to the west, at Dead Man's Corner, is another cypress site in a former channel of the Wabash River. The next nearest cypress is about 3 miles east of Mt. Vernon. Also eastward it is found near Evansville in Vanderburg County and along Cypress Creek in Warrick County where it reaches its known limit. To the north cypress is absent in Gibson County but is present in the Little Cypress Swamp in the "pocket" of Knox County where it reaches its northernmost station. See figure 3.

The Investigation

Twenty-five 100 sq.m. quadrats were scattered evenly in the forest at the southwest side of the lake. Table 1 gives a list of the trees, shrubs and woody vines encountered in the survey according to frequency classes (Cain, 1932). The trees most evenly distributed through the woods, of highest frequency, are *Acer saccharinum* (88%), *Taxodium distichum* (84%), *Salix nigra* (44%), *Ulmus fulva* (40%), and *Carya Pecan* (40%). Other woody plants of high frequency are *Cephalanthus occidentalis* (72%), *Rhus Toxicodendron* (56%), and *Vitis aestivalis* (44%).

TABLE 1

Frequency of woody plants, Cypress Swamp Forest, Hovey Lake, 25 quadrats @ 10 x 10 m.

Life-form	Species (20)	Frequency per cent
Class A (1-20 %)	(8 species)	**40**
Vine	*Smilax rotundifolia* L.	4
Tree	*Celtis laevigata* Willd.	12
Tree	*Fraxinus lanceolata* Borck.	12
Tree	*Populus deltoides* Marsh.	12
Tree	*Betula nigra* L.	20
Tree	*Fraxinus profunda* Bush.	20
Vine	*Menispermum canadense* L.	20
Tree	*Platanus occidentalis* L.	20
Class B (21-40%)	(6 species)	**30**
Tree	*Foresteria acuminata* (Michx.) Poiret	28
Vine	*Vitis rubra* Michx.	32
Vine	*Ampelopsis cordata* Michx.	36
Vine	*Campsis radicans* (L.) Seemann	40
Tree	*Carya Pecan* (Marsh.) Eng. & Graeb.	40
Tree	*Ulmus fulva* Michx.	40
Class C (41-60%)	(3 species)	**15**
Tree	*Salix nigra* Marsh.	44
Vine	*Vitis aestivalis* Michx.	44
Vine	*Rhus Toxicodendron* L.	52
Class D (61-80%)	(1 species)	**5**
Shrub	*Cephalanthus occidentalis* L.	72
Class E (81-100 %)	(2 species)	**10**
Tree	*Taxodium distichum* (L.). L. C. Rich.	84
Tree	*Acer saccharinum* L.	88

The number of woody species per quadrat averaged 7, ranging from 2 to 10 species in a plot.

Table 2 gives the density by d.b.h. of six tree species. The other trees listed in Table 1 were not represented by stems 1 inch d.b.h. or more. *Acer saccharinum* has the heaviest distribution up to 1 foot d.b.h. *Salix nigra* shows a grouping from 9 to 19 inches d.b.h. *Populus deltoides* and *Carya Pecan* show a scattering through the middle sizes from 1 to 2½ feet d.b.h. *Taxodium distichum* is practically absent in small reproduction under 1 inch d.b.h. but ranged through all diameters up to one tree of 50 inches d.b.h., although the smaller sizes are not normally abundant. This table shows a total of 206 stems per acre above 1 inch d.b.h. and a total basal area of about 250 sq. ft. per acre. The mature trees average about 100 feet high.

TABLE 2

Density of six species by D. B. H. in inches in Cypress Swamp Forest, Hovey Lake, 25 quadrats @ 10 x 10 m.

D.B.H.	A.S.	T.D.	P.D.	C.P.	S.N.	B.N.	Total
1	2	12	--	--	--	1	15 per acre
2	7	1	--	--	--	--	8
3	8	--	--	--	--	--	8
4	9	--	--	--	--	--	9
5	1	--	--	--	--	--	1
6	2	--	--	--	--	--	2
7	2	1	--	--	--	--	3
8	4	--	--	--	--	--	4
9	1	1	--	--	1	--	3
10	3	--	--	--	3	--	6
11	1	1	--	--	3	--	5
12	1	1	--	--	3	--	5
13	4	--	1	--	2	--	7
14	--	--	--	--	2	--	2
15	2	4	--	--	5	--	11
16	--	--	--	--	6	--	6
17	1	2	1	1	3	--	8
18	1	1	--	1	1	--	4
19	--	1	--	--	1	--	2
20	1	--	--	1	--	--	2
21	--	1	2	--	--	--	3
23	1	2	--	--	--	--	3
24	--	2	--	1	--	--	3
29	--	1	--	1	--	--	2
30	--	--	1	1	--	--	2
32	--	1	--	--	--	--	1
35	1	--	--	--	--	--	1
36	--	1	--	--	--	--	1
50	--	1	--	--	--	--	1
Total no. of stems	52	35	5	6	30	1	128 206 per acre
Basal area per acre	28.5 46.1	63.1 101.8	12.2 19.7	18.2 29.3	33.4 53.9	-- --	155.48 sq. ft. 250.77 per acre

AS, *Acer saccharinum;* TD, *Taxodium distichum;* PD, *Populus deltoides;* CP, *Carya Pecan;* SN, *Salix nigra;* BN, *Betula nigra.*

Tables 3 and 4 show the observations from the quadrats on the shrub and herb strata as to coverage and height. It is obvious that these layers are spotty as to the extent of cover within them, and especially, as to height, depending on the mosaic of component species. Considering that the arborescent stratum presents almost 100 per cent coverage and very dense shade, that the herb coverage should be so high—40 per cent of the quadrats showing class 5 coverage in the herb stratum—speaks for the shade-tolerant nature of the species of the inferior strata and the rich character of the soil.

TABLE 3

Coverage in the herb and shrub strata, Cypress Swamp Forest, Hovey Lake, 25 quadrats @ 10 x 10 m.

Herb Stratum		Shrub Stratum	
Cover Class	No. of Quads	Cover Class	No. of Quads
1 (0-5%)	6	1	10
2 (6-25%)	6	2	5
3 (26-50%)	2	3	6
4 (51-75%)	1	4	4
5 (76-100%)	10	5	0
Average: Class 3, 44%.		Class 2, 23%.	

TABLE 4

Height of the herb and shrub strata, Cypress Swamp Forest, Hovey Lake, 25 quadrats @ 10 x 10 m.

Herb Stratum		Shrub Stratum	
Height in feet	No. of quads.	Height in feet	No. of quads
0.5	3	1.0	6
1.0	6	2.0	3
1.5	2	3.0	3
2.0	5	4.0	7
2.5	2	5.0	2
3.0	2	6.0	2
3.5	3	8.0	1
3.0	1	12.0	1
Average height, 1.8 ft.		Average height, 3.6 ft.	

The shrub stratum is marked principally by *Cephalanthus occidentalis* and *Foresteria acuminata* (which more often behaves as a shrub than as a tree in this region) and several rank growing vines as *Vitis aestivalis, V. rubra, Menispermum canadense,* etc. The herb layer is marked by many species growing in luxuriant profusion, including: lizard's tail, jewel weed, clear weed, bugle weed, nettles, smart weeds, wild cucumber, etc. Figure 1 is a coverage-stratification diagram of the woods as determined by the quadrat study. There is no soil stratum of lichens and mosses.

A second series of 100 sq. m. quadrats, 10 in number, were laid out along the outlet between the lake and the Ohio River. These data are summarized for cypress in Table 5, which shows a strong contrast with the previous set of plots. There is an abundance of young plants here by the water's edge, but

as in the case of the woods generally, (Table 2), young trees of 1 to a few inches d.b.h. are abnormally few. These figures show that in the immediate vicinity of the outlet the conditions for seed germination and establishment are good (1932) and have been for a decade or more. There is, however, a high mortality for the first few years. There is no ready explanation in the survey data for the gap between young reproduction and mature trees, even here by the outlet, much less in the woods generally.

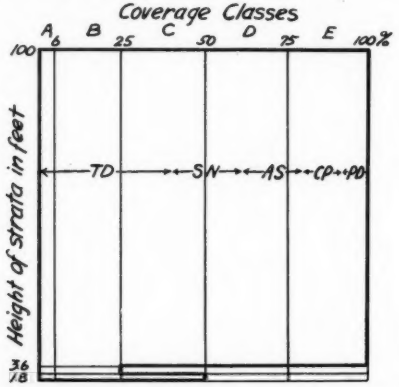

Fig. 1. A coverage-stratification diagram representing that portion of the forest sampled by the quadrats. The heavy line on the right indicates the coverage class for each of the three strata. In the tree stratum the percentage of the total basal area for five species is indicated. Symbols are the same as in Table 2.

In the lake proper there are several old, over-mature, flat-topped, and stag-headed cypress, but in the channel of the outlet, (also in the inlet and certain shallow parts of the eastern basin) adjacent to the ten plots referred to above, and under water most of the year, are several healthy trees of the following dimensions.

Plot 1	12 inches d.b.h.	2 trees
Plot 4	12 inches d.b.h.	2 trees
Plot 4	24 inches d.b.h.	1 tree
Plot 5	2 inches d.b.h.	1 tree
Plot 6	12 inches d.b.h.	1 tree
Plot 7	2 inches d.b.h.	1 tree
Plot 7	24 inches d.b.h.	1 tree
Plot 8	22 inches d.b.h.	1 tree
Plot 8	26 inches d.b.h.	1 tree
Plot 9	34 inches d.b.h.	2 trees
Plot 9	48 inches d.b.h.	1 tree
Plot 9	60 inches d.b.h.	1 tree

It will be noticed that these trees are nearly all 1 foot d.b.h. or over.

TABLE 5

Cypress along outlet of Hovey Lake, 10 quadrats @ 10 x 10 m. Each quadrat had one edge at the water line.

Height in feet	Quadrat number 1	2	3	4	5	6	7	8	9	10	Total
1	101	30	91	164	41	11	28	27	8	7	508
2	16	16	8	13	31	9	6	1	–	–	100
3	3	12	4	5	13	2	9	1	–	–	49
4	–	6	1	3	4	1	2	–	–	–	17
5	1	–	1	–	1	1	1	–	–	–	5
6	–	2	–	–	–	–	–	–	–	–	2
7	–	3	–	–	–	–	–	–	1	–	4
8	–	–	1	1	–	–	–	–	–	–	2
											687
Diameter in inches											
1	–	1	–	1	–	–	–	–	–	–	2
2	–	–	–	1	–	–	–	–	–	–	1
16	–	–	–	–	–	–	–	–	–	1	1
18	–	–	–	–	–	–	–	–	–	1	1
21	–	–	–	–	–	–	–	–	–	1	1
22	–	–	–	–	–	–	–	–	–	1	1
26	–	–	–	–	–	–	–	–	–	1	1
35	–	–	–	–	–	–	–	–	1	–	1
											9

Total number of trees on 1,000 sq. m. 696
Total of 2,900 trees per acre

Discussion

Some observations on the conditions necessary for cypress germination and establishment have been made. Demaree (1932), from work on the "Sunken Lands" of Arkansas, concluded that seeds must germinate on emerged soil and reach a greater height than the next high water (providing it is of more than a *few days* duration) if they are to become established. Should flood waters be low for two or three years the plants might grow enough to keep above water (most of the time) and survive. Welch (1932) from greenhouse experiments found that seedlings could survive submergence for *several weeks* but made no growth while submerged. Mattoon (1915) says that in early stages cypress is very exacting and successfully establishes itself only in situations of very abundant moisture, but if kept continuously submerged will not germinate. Seed-bed requirements are a very abundant supply of moisture maintained for 1 to 3 months. The young seedling is almost semi-hydrophytic in its early stages and develops well in saturated soil, although it does better where there is some drainage.

From the somewhat scanty information available, considering the wide range, botanical interest, and economic importance of the species, one must conclude that a certain, rather particular, set of conditions is necessary for good cypress reproduction. Good seed years (which occur in about 3 year

cycles, Mattoon, 1915) must coincide with high enough water to soak the seeds 1 to 3 months for good germination, after which there must be no prolonged submergence for a sufficient period (1 to a few years) to allow the saplings to reach above the height of the next prolonged inundation.

Mattoon (1915), Kearney (1901) and others point out the poor reproduction or absence of it on older silted-in swamp areas where mature trees are found. This is due to the general absence of seed-bed conditions referred to above and the greater competition with broad-leaved species which are less exacting in conditions for germination and establishment, and more shade tolerant. *Taxodium* would seem to represent an edaphic climax where swampy conditions are maintained but with silting-in would give way in succession to broad-leaved species. Harper (1912) observes the general absence of cypress from streams and ox-bow lakes where the average seasonal fluctuations in water level are more than 10 to 12 feet. He points out that the trunks elsewhere usually emerge from the ground just about the low-water mark.

In the cypress woods of Hovey Lake one must conclude that the general absence of reproduction, except in the immediate vicinity of the outlet, is due to the absence of seed-bed conditions as described previously. This is partly due to silting-in of the portions of the old woods farthest from the present lake margin, and partly due to human influences which control largely the water level fluctuations except during periods of unusual high water or severe drought. Agricultural levees constructed several years ago prevent the normal influence of the rise and fall in the Ohio River on the water level of this ox-bow lake. Also, a dam and lock constructed on the outlet enables the water level in the lake to be regulated to a certain extent.

Kearney (1901) and others have commented on the slowness with which cypress comes back after lumbering. This, plus the effects of drainage canals and natural silting-in, works toward the decrease of cypress in Indiana swamp forests as time goes on. It is little wonder that Deam says cypress is destined to generally disappear from its original stations in the Lower Wabash Valley, as it already has in the main.

Correlative evidence is found in the nature and development of buttresses and knees. Cypress buttresses at Hovey Lake are of the conical type and only moderately developed (Fig. 2). This is also true of cypress at other Indiana stations (Fig. 3). Knees are generally absent although a few low ones are found in places near the water's edge. Several interesting comments on these matters are found in the literature. Very convincing is the recent paper by Kurz and Demaree (1934) where they advance the theory that "Buttress development is a response to the simultaneous presence of water and air.... It would seem, therefore, that the form of any particular buttress will depend upon the frequency as well as duration with which its various horizons are subjected at once to water and air." Knees are attributed to the same combination of factors. They are generally absent in deep water and regions where inundation is the exception or of brief duration. They are well-developed in intermediate conditions (Fig. 4) and their height (as

Fig. 2. A cypress at Hovey Lake showing the typical form of the buttress and the general absence of knees. This tree is nearly five feet in diameter breast high. Photo by S. A. Cain.

of marked buttress development) is regulated by the average height of the "water and air" action. Other authors, Kearney (1901), Harper (1905, 1912), and Mattoon (1915) state that the height of knees correlates generally with the average high-water level.

One would conclude then, that the low, moderately-developed, conical buttresses and the low, infrequently-developed knees point to a general absence of conditions described previously as necessary for good seed-bed conditions.

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Fig. 3. A large cypress, over six feet in diameter breast high, at Little Cypress Swamp, Knox County, Indiana. Here again the typically slight buttress development and scanty knee production is illustrated. Photo by S. A. Cain.

Fig. 4. Cypress at Reelfoot Lake near the Mississippi River in western Tennessee showing typical knee development for a site with a zone of a few feet of water-air action. Photo by S. A. Cain.

Fig. 4. Cypress at Reelfoot Lake near the Mississippi River in western Tennessee showing typical knee development for a site with a zone of a few feet of water-air action. Photo by S. A. Cain.

FRANCIS DANIELS' FLORA OF COLUMBIA, MISSOURI

BENJAMIN FRANKLIN BUSH

In a previous paper, (Amer. Midl. Nat. **12:** 185, 343, 1931) I reported the results of my examination on the grasses as well as on the *Carices* of Daniels' Flora of Columbia, Mo. (Univ. Mo. Stud. Sci. Ser. **1** (2), 1907). This report covers the greater number of specimens upon which Daniels based the remaining part of his *Flora.* Since this work appeared in print, some changes have been made in specific names. Further research on certain genera, especially on *Crataegus, Malus, Rubus, Rosa, Prunus* and *Carya,* has resulted in additions to the number of species known to occur in the state. It has also been discovered that many species supposed to occur in Missouri are not found in the state, and, consequently, have been falsely reported from Boone County. This is especially true of species of the genera *Equisetum, Tradescantia, Polygonatum, Celtis, Aesculus, Acer* and *Viburnum.*

In this report, I am presenting Daniels' generic and specific names and his numbers just as he has given them in his *Flora,* so that reference to the species can be readily made.

14. *Ophioglossum vulgatum* L.—The specimens so named by Daniels belong to *O. Engelmannii,* a species abundant in rocky barrens in all southern, eastern, and western Missouri. However, *O. vulgatum* does occur in several counties in the lowlands of extreme southeastern Missouri.

17. *Equisetum pratense* Ehrh.—The specimens so-named were at first labeled *E. sylvaticum* by Daniels, and this name was later changed to *E. pratense* by him; but the specimens are *E. arvense. E. pratense* is not now known to occur in the State.

18. *Equisetum hyemale* L.—Daniels' specimens so-called are the abundant species *E. laevigatum. E. hyemale,* the European species, is not now gknown to occur in Missouri. *E. robustum,* the tall, robust, abundant species of the Missouri River bottoms, is not given by Daniels in his *Flora;* but it has been collected at Rocheport in 1928 and 1929.

19. *Equisetum variegatum* Schleich—The specimens so-called by Daniels were referred to the abundant species *E. laevigatum. E. variegatum* does not, so far as is now known, occur in Missouri.

25. *Potamogeton Hillii* Morong—All of the seven sheets of specimens collected by Daniels, and so-named by him, prove to be *P. foliosus,* a species not mentioned in his *Flora.*

152. *Cyperus Hallii* Britton—The four sheets of specimens so-named by Daniels are the abundant species *C. esculentus.*

155. *Cyperus speciosus parvus* (Boeckl.) Britton—The specimens so-named by Daniels are referred to the common *C. speciosus.*

160. *Scirpus lacustris* L.—The specimens so-named by Daniels have been referred to *S. validus*. The European *S. lacustris* does not occur in Missouri.

163. *Heleocharis acuminata* (Muhl.) Nees—The specimens so-named by Daniels are referred to *H. obtusa*.

165. *Heleocharis intermedia* (Muhl.) Schultes—The specimens so-called by Daniels are referred to *H. obtusa*.

166. *Heleocharis glaucescens* (Willd.) Schultes—The specimens so-named by Daniels are referred to *H. obtusa*.

167. *Heleocharis palustris* (L.) R. & S.—The specimens so-named by Daniels are referred to *H. obtusa*.

168. *Heleocharis Engelmannii* Steud.—The specimens so-called by Daniels are referred to *H. obtusa*.

169. *Heleocharis ovata* (Roth) R. & S.—The specimens so-named by Daniels are referred to *H. obtusa*.

220. *Lemna Valdiviana* Philippi—No specimens of this species under any name were found in the Daniels collection from Columbia.

223. *Commelina nudiflora* L.—No specimens under any name were found in the Daniels collection from Columbia.

224. *Commelina virginica* L.—All of Daniels' specimens so-called are referred to *C. communis*.

227. *Tradescantia reflexa* Raf.—Specimens labeled *T. brevicaulis*, and *T. virginica* are referred to this species. *T. virginica*, however, was collected in Boone County in 1926.

231. *Juncus aristatulus* Michx.—The specimens so-called by Daniels are referred to *J. marginatus*.

235A. *Juncus acuminatus legitimus* Engelm.—The specimens so-called by Daniels are referred to *J. acuminatus*.

236. *Juncus scirpoides* Lam.—The specimens so-called by Daniels are referred to *J. acuminatus*.

238. *Luzula campestris* (L.) DC.—No specimens of this species were found in the Daniels collection, although it probably occurs in Boone County.

247. *Erythronium americanum* Ker.—The basis of this species in Daniels' *Flora* is an old specimen of Swallow's, without date or station, and possibly not from Boone County. However, this species is found in rich woods along small streams in the Ozark counties.

255. *Polygonatum biflorum* (Walt.) Ell.—No specimens of this species under any name were found in the Missouri collection. This species occurs in the Southeastern States and has not yet been found within the range of *Gray's Manual*. A narrow-leaved variety of *P. commutatum* has been generally mistaken for *P. biflorum*.

282. *Carya porcina* Nutt.—No specimens of this species were found under any name in the University collection from Missouri; and I suspect that trees of *C. arkansana* must have been found and mistaken for *C. porcina*. Trees of *C. arkansana* have since been found in Boone County, and Daniels does

not mention this species in his *Flora*. However, *C. porcina* does occur on high sand-hills in Dunklin and Butler Counties, in southeastern Missouri.

287a. *Salix nigra falcata* (Pursh) Torr.—All the specimens so-named by Daniels are referred to *S. nigra*, the abundant species along the Missouri River bottoms.

289. *Salix amygdaloides* Anders—No specimens of this species under any name were found in the Daniels collection; but as it is very common in the Missouri River bottoms, it must undoubtedly occur in Boone County.

290. *Salix alba* L.—No specimens of the European *S. alba* were found in the University collection, all those so-named by Daniels being the well-known *S. Wardii*. *S. alba* does not appear to have become introduced in Missouri so far as now known.

293a. *Salix cordata angustata* (Pursh) Anders—No specimens of this variety under any name were found in the Daniels collection, all those so-named being *S. Wardii*.

314. *Celtis occidentalis* L.—No specimens of the Eastern Hackberry were found in the University collection from Missouri, all those collected by Daniels being the common *C. canina*.

315. *Celtis georgiana* Small—No specimens of this species were found in the Daniels collection, all those so-named being *C. laevigata*, a species he did not recognize and did not mention in his *Flora*.

317. *Morus nigra* L.—No specimens of this species under any name were found in the University collection from Columbia, and I have no knowledge of its having escaped from cultivation in Missouri.

327. *Urtica dioica* L.—No specimens of this species under any name were found in the University collection from Missouri.

328. *Asarum ambiguum* (Bicgknell) Daniels—No specimens of this species were found in the Daniels collection, but Daniels undoubtedly collected *A. reflexum* and mistoogk it for this species.

330. *Rumex salicifolius* Weinm.—No specimens of this abundant species were found in the Daniels collection.

337. *Polygonum littorale* Link—The specimens so-named by Daniels have been referred to *P. buxiforme* Small. See Rhodora **59:** 362.

342. *Polygonum hydropiperoides* Michx.—No specimens of this species were found in the Daniels collection.

363. *Amaranthus paniculatus* L.—No specimens of this species were found in the Daniels collection.

368. *Amaranthus albus* L.—No specimens of this abundant species were found in the Daniels collection, and the one named this (*A. graecizans* L.) has been referred to *A. blitoides*. See Rhodora **35:** 362.

372. *Mirabilis decumbens* (Nutt.) Daniels—All the specimens so-called in the Daniels collection are referred to the common *Allionia albida*.

384. *Cerastium semidecandrum* L.—The specimens so-called in the Daniels collection are referred to the common *C. vulgatum*.

386. *Cerastium brachypodum* (Engelm.) Robinson—The specimens so-named by Daniels are referred to the common *C. viscosum*.

412. *Thalictrum purpurascens* L.—All the specimens so-named by Daniels were referred to *T. dasycarpum*, a species not recognized at the time Daniels prepared his *Flora*.

435. *Barbarea stricta* Andrz.—The specimens so-named by Daniels are referred to *B. vulgaris*.

458. *Ribes gracile* Michx.—Daniels evidently did not realize that this is the same as *R. missouriense*.

463. *Physocarpus missouriensis* Daniels—The specimens so-called by Daniels are referred to *P. intermedius*.

467. *Pyrus angustifolia* Ait.—No specimen of this species under any name was found in the University collection from Missouri, all the specimens examined being referred to *Malus lancifolia*, a species Daniels does not mention in his *Flora*.

468. *Pyrus ioensis* (Wood) Bailey—No specimens so-called by Daniels were found in the University collection; but there are two sheets of it in his collection, one labeled *P. coronaria*, a species he does not mention in his *Flora*, and one named *P. angustifolia*.

471. *Mespilus punctata* (Jacq.) Willw.—Daniels' single collection so-named is *Crataegus fecunda*, a common species in eastern Missouri. *C. punctata* is not known to occur in Missouri.

473. *Mespilus Eggertii* (Britton) Daniels—Daniels was evidently unaware that this is the same as *Crataegus coccinioides*, but no specimens were found in his collection. However, the species is common in eastern Missouri.

474. *Mespilus viridis* (L.) Sweet—Two sheets of specimens so-named by Daniels are referred to *Crataegus consueta*, and one sheet is an unknown species in the *Punctatae*-group. *C. viridis* is common in the lowlands of southeastern Missouri, also in southwestern Missouri.

475. *Mespilus nitida* (Engelm.) Daniels—The five sheets of specimens so-named by Daniels are referred to an undetermined *punctatae* species. *Crataegus nitida* occurs in the big bottoms along the Mississippi River near Saint Louis and southward.

476. *Mespilus coccinea* (L.) Willd.—The ten sheets of specimens so-named by Daniels are referred to *Crataegus patrum*, a species common in the Saint Louis district. *C. coccinea* is not now known to occur in Missouri.

477. *Mespilus rotundifolia* (Ehrh.) Daniels—The single sheet of specimens so-named by Daniels is *Crataegus patrum*. *C. rotundifolia* is not now known to occur in Missouri.

478. *Mespilus macracantha* (Lodd.) Wenzig—The one specimen so-named in the Daniels collection is *Crataegus patrum*, mentioned above twice. *C. macracantha* occurs in extreme northeastern Missouri.

480. *Mespilus Biltmoreana* (Beadle) Daniels—No specimen so-named by Daniels is in his collection, but there is a specimen collected by Sweet labeled

M. Biltmoreana that is *Crataegus tomentosa*. *C. Biltmoreana* is not known to occur in Missouri.

481. *Mespilus campestris* (Britton) Daniels—Eight sheets of specimens, all of Daniels' collecting, and so-named by him, are *Crataegus tomentosa*. *C. campestris* occurs in rocky barrens on the prairies in western Missouri and Kansas.

483. *Mespilus Chapmanii* (Beadle) Daniels—The two sheets of specimens collected by Daniels, and so-named by him, are *Crataegus tomentosa*. However, *C. Chapmanii* occurs in the Ozark region in southern Missouri.

484. *Mespilus dispessa* (Ashe) Daniels—The two sheets so-named by Daniels are both *Crataegus tomentosa*. *C. dispessa* occurs so far as known only in Shannon County.

494. *Geum strictum* Ait.—No specimens of this species were found in the Daniels collection.

501. *Rosa humilis* Marsh—No specimens of this species under any name were found in the Daniels collection.

501a. *Rosa humilis villosa* Best—No specimens so-named were found in the Daniels collection from Misouri.

502. *Rosa Woodsii* Lindl—No specimens of this species under any name were found in the University collection from Missouri. *R. Woodsii* is not known to occur in the State.

503. *Rosa setigera* Michx.—No specimens of typical *R. setigera* under any name were found in the Daniels collection from Missouri, all those so-named being the var. *tomentosa*.

504. *Prunus americana* Marsh.—No specimens of this species under any name were found in the Daniels collection from Missouri. *P. americana* is an Atlantic coastal species and does not occur in Missouri.

514. *Cassia marilandica* L.— All the specimens collected by Daniels and so-named by him are *C. Medsgeri*, a species not mentioned by Daniels in his *Flora*. *C. marilandica* is an Atlantic species and is not known to occur in Missouri.

531. *Trifolium medium* L.— All the specimens so-named by Daniels are the common *T. pratense*.

535. *Amorpha nana* Nutt.—Daniels' specimens so-named are merely a starved state of the common *A. canescens*.

547. *Desmodium pauciflorum* (Nutt.) DC.—No specimens of this species under any name were found in the Daniels collection from Missouri. However, *D. pauciflorum* does occur in southeastern Missouri.

552. *Desmodium longifolium* (T. & G.) Daniels—Daniels' specimens so-named are the common *D. Dillenii*.

559. *Desmodium rigidum* (Ell.) DC.—All of Daniels' specimens so-named by him are the common *D. Dillenii*.

560. *Lespedeza repens* (L.) Bart.—The two specimens so-named by Daniels are *L. virginica* and *L. prairea*, the latter species not mentioned by him in his *Flora*.

562. *Lespedeza violacea* (L.) Pers.—No specimens so-named were found in the Daniels collection from Missouri.

563. *Lespedeza Stuvei* Nutt.—Specimens labeled thus were referred to *L. violacea*.

564. *Lespedeza frutescens* (L.) Britton—Specimens so-labeled were referred to *L. violacea*.

594. *Euphorbia humistrata* Engelm.—No specimens of this species under any name were found in the Daniels collection from Missouri.

612. *Acer saccharinum* Wang.— No specimens of this species were found in the Daniels collection. I assume that Daniels intended to designate the Eastern Sugar Maple, a species that does not occur in Missouri.

613. *Acer barbatum* Michx.—There are two specimens labeled *A. Saccharum barbatum* in the Daniels collection. The tree Daniels had in mind I later named *A. barbatum* var. *glaucum*.

617. *Aesculus lutea* Wang.—No specimens of this species from Missouri were found in the University Herbarium, and it is not known to occur west of the Mississippi River.

621. *Rhamnus cathartica* L.—One specimen of this species, labeled *Ligustrum vulgare*, was found in the Daniels collection from Columbia. See Rhodora **59**: 363.

625a. *Vitis cinerea canescens* (Engelm.) Bailey—All of the specimens so-named by Daniels are referred to *V. cinerea*.

628. *Vitis rubra* Michx.—All of the specimens so-named by Daniels are the species that has been passing for *V. vulpina*.

629. *Quinaria quinquefolia* (L.) Koehne—No specimens of this species were found in the Daniels collection from Boone County.

640. *Hypericum subpetiolatum* Bickn.—All of the specimens so-named by Daniels are the common *H. maculatum*.

641. *Hypericum pseudomaculatum* Bush—No specimens if this species under any name were found in the Daniels collection.

644. *Hypericum nudiflorum* Michx.—No specimens of this species under any name were found in the University collection from Missouri, all that were so-named being *H. cistifolium*. *H. nudiflorum* is a species of the southeastern States and has not yet been found in the range of *Gray's Manual*.

653. *Viola palmata* L.—No specimens of *V. palmata* were found in the Daniels collection from Missouri.

656. *Viola domestica* Bicknell.—No specimens so-named were found in the Daniels collection from Boone County.

657. *Viola cuspidata* Greene—No specimens so-named were found in the Daniels collection.

659. *Viloa cucullata* Ait.—No specimens of this species under any name were found in the Boone County collection.

662. *Viola pubescens* Ait.—No specimens of this species were found in the Missouri collection. *V. pubescens* is an eastern species that does not get into Missouri.

673. *Epilobium adenocaulon* Haussk.—Ayy of Daniels' specimens so-named are referred to *E. coloratum*, a species he does not mention in his *Flora*.

674a. *Oenothera biennis grandiflora* (Ait.) Lindl.—No specimens of this variety were found in the University collection from Missouri, and it is not known to occur in the State.

687. *Chaerophyllum floridanum* (C. & R.) Bush.—No specimens of this species under any name were found in the Daniels collection.

707. *Cornus Drummondii* Meyer—No specimens of this species under any name were found in Daniels' collection from Missouri, all those so-named being referred to *C. asperifolia*.

714. *Lysimachia Nummularia* L.—No specimens of this species were found in the Boone County collection.

717. *Steironema heterophyllum* (Michx.) Raf.—No specimens of this species were found in the Daniels collection from Missouri

724. *Fraxinus nigra* Marsh.—No specimens of this species were found in the University collection from Missouri. *F. nigra* has often been cited for Missouri, but it is yet unknown to the State.

730. *Apocynum urceolifer* Miller—The specimens so-named by Daniels are referred to *A. album*.

731. *Apocynum hypericifolium* Ait.—The specimens so-named by Daniels are the abundant species *A. album*.

732. *Apocynum cannabinum* L.—The specimens so-named by Daniels are referred to *A. album* and *A. pubescens*.

736. *Asclepias decumbens* L.—All of the specimens so-named by Daniels are the very common *A. tuberosa*. *A. decumbens* does not occur in Missouri, so far as is known.

764. *Lithospermum officinale* L.—No specimens of this species were found in the Boone County collection, Daniels' single specimen so-named being referred to *L. angustifolium*.

766. *Onosmodium molle* Michx.—No specimens of this species under any name were found in the Daniels collection, the few specimens so-named being *O. occidentale* and *O. subsetosum*, two species not recognized by Daniels and put into his *Flora*.

790. *Monarda fistulosa* L.—No specimens so-named were found in the

Daniels collection from Missouri, but there are several specimens labeled *M. mollis* that are *M. fistulosa.*

792. *Monarda media* Willd.—No specimens of this species under any name were found in the University collection from Missouri, all those so-named being *M. mollis. M. media* is not known to occur in the State.

800. *Lycopus communis* Bicknell—No specimens of this species under any name were found in the University collection from Missouri, all those so-named being referred to *L. americanus. L. communis* is not known to occur in Missouri.

801. *Lycopus rubellus* Moench—The specimen so-named by Daniels has been referred to *L. americanus.*

802. *Lycopus lucidus* Turcz.—The two sheets of specimens collected by Daniels are both *L. americanus. L. lucidus* is not known to occur in Missouri.

814. *Physalis nyctaginea* (Dunal.) Rydb.—The specimens so-named by Daniels were referred to the common *P. heterophylla.*

832. *Pentstemon hirsutus* (L.) Willd.—All of Daniels' specimens so-named were referred to *P. pallidus,* a species he does not mention in his *Flora.*

833. *Pentstemon Pentstemon* (L.) Britton—The sheets of specimens so-named by Daniels are the common *P. Digitalis* and *P. tubiflorus.*

842. *Veronica serpyllifolia* L.—The basis of this report consists of two sheets labeled thus. They are specimens of *V. peregrina* and *V. arvensis.*

849. *Gerardia grandiflora* Benth.—The specimens so-named by Daniels are *G. grandiflora serrata.*

850. *Gerardia flava* L.—The specimens so-named by Daniels are *G. grandiflora serrata.*

858a. *Ruellia strepens micrantha* (Engelm. & Gray) Britton—Daniels' specimens so-named are the common *R. strepens.*

861. *Plantago major* L.—No specimens of this species were found in the Daniels collection from Missouri.

866. *Plantago occidentalis* Decne.—All of Daniels' specimens so-named are the abundant *P. virginica.*

867. *Plantago spinulosa* Decne.—All of Daniels' specimens so-named are reduced forms of the abundant *P. aristata.*

873. *Galium trifidum* L.—No specimens of this species under any name were found in the collection from Missouri, all those so-named being *G. tinctorium.*

880. *Viburnum dentatum* L.—No specimens of this species under any name were found in the Daniels collection from Missouri; but there are specimens in the University Herbarium from the Pinnacles, *V. affine* Bush, which I assume to be the same thing Daniels found there. *V. dentatum* is not known to occur in Missouri.

881. *Viburnum Lentago* L.—No specimens of this species under any name were found in the University collection from Missouri. It is not yet certain that *V. Lentago* occurs in Missouri.

882. *Viburnum prunifolium* L.—No specimens labeled thus were found in Daniels' Boone County collection to be *V. prunifolium*, all those so-named being *V. rufidulum*.

883. *Viburnum rufotomentosum* Small—Specimens of this species were labeled *V. prunifolium* by Daniels.

886. *Lonicera glauca* Hill—No specimens in Daniels' collection from Missouri named *L. glauca* were found, but there are two sheets labeled *L. dioica* from the Waterworks Dam.

887. *Lonicera grata* Ait.—No specimens of *L. grata* under any name were found in the Daniels collection from Missouri, all three specimens so-named being *L. Sullivantii*, a species not mentioned in his *Flora*. *L. grata* has been cited for Missouri by Robinson and Fernald in *Gray's Manual*, by Britton and Brown in the *Illustrated Flora*, and by other authors; but I have not seen any specimens of it from the State.

901. *Lobelia leptostachys* A. DC.—No specimens of this species under any name were found in the Daniels collection, all those so-named being referred to *L. spicata*.

905. *Vernonia Duggariana* Daniels—Daniels' specimens so-named were referred to the common *V. Baldwinii*.

906. *Vernonia flavipappa* Daniels—Daniels' specimens so-named were referred to *V. Baldwinii*.

907. *Vernonia parthenioides* Daniels—All the specimens so-named by Daniels I have referred to *V. Baldwinii*. Rickett (Univ. Mo. Stud. **6** (1): 81) reduced the species to varietal status.

908. *Vernonia peralta* Daniels—All the specimens so-named by Daniels were referred to *V. Baldwinii*.

909. *Vernonia pseudobaldwinii* Daniels—All the specimens so-named by Daniels were referred to *V. Baldwinii*.

910. *Vernonia pseudodrummondii* Daniels—All the specimens so-named by Daniels were referred to the abundant *V. interior*.

913. *Vernonia Reedii* Daniels—All of the specimens so-named by Daniels were referred to the common *V. missurica*.

915. *Vernonia chrysopappa* Daniels—The specimens so-named by Daniels were referred to the common lowland *V. fasciculata*.

917. *Eupatorium purpureum* L.—All of Daniels' specimens so-named are the common *E. Holzingeri* Rydb. *E. purpureum* does not occur in Missouri so far as is known.

924. *Eupatorium aromaticum* L.—All of Daniels' specimens so-named

were referred to the common *E. urticaefolium*. *E. aromaticum* is not known to occur in Missouri.

933. *Solidago rugosa* Mill.—All of the specimens so-named by Daniels are the common *S. ulmifolia*.

935. *Solidago juncea* Ait.—No specimens of this species under any name were found in Daniels' collection from Missouri.

936a. *Solidago serotina gigantea* (Ait.) Gray—No specimens of this variety under any name were found in the Daniels collection from Missouri.

937. *Solidago canadensis* L.—Many of the specimens so-named by Daniels were referred to the species generally accepted by the Manuals and Floras as *S. altissima*, a species Daniels does not mention in his *Flora*. The remainder of the specimens were placed in the var. *gilvocanescens*.

937a *Solidago canadensis procera* (Ait.) T. & G.—Daniels' specimens so-named are the abundant var. *gilvocanescens*.

937b. *Solidago canadensis scabriuscula* Porter—All of Daniels specimens so-named were referred to the common *S. altissima*.

951. *Aster dumosus* L.—No specimens of the species were found in the Daniels collection from Missouri.

955. *Aster simplex* Willd.—No specimens of this species under any name were found in the Daniels collection from Missouri.

957. *Aster prenanthoides* Muhl.—The specimens so-named by Daniels were referred to the abundant *A. paniculatus*.

967. *Antennaria calophylla* Greene—The specimens so-labeled by Daniels were referred rather doubtfully to *A. plantaginifolia*, but they probably do not belong to that species.

969. *Gnaphalium uliginosum* L.—Daniels' specimens so-named are the common species, *E. purpureum*.

981. *Ambrosia integrifolia* Muhl.—Daniels' one specimen probably belongs to *A. striata*, an apparently distinct Missouri species which has been passing as *A. trifida*.

985. *Xanthium pennsylvanicum* Wallr.—No specimens of this species under any name were found in the Daniels collection.

986. *Xanthium speciosum* Kearney—No specimens of this species under any name were found in the Daniels collection.

998. *Rudbeckia Tagetes* James—The one specimen so-labeled has been referred to *Lepachys pinnata*. *R. Tagetes* is not known to occur in Missouri.

1000a. *Helianthus hirsutus trachyphyllus* T. & G.—All of the specimens so-named by Daniels were referred to *H. hirsutus*.

1002. *Helianthus macrophyllus* (Willd.) Daniels—Daniels' specimens so-named were all referred to *H. strumosus*.

1003. *Helianthus tuberosus subcanescens* Gray—All of Daniels' specimens so-named were referred to *H. tuberosus*, a species he does not list in his *Flora*

1009. *Coreopsis discoidea* T. & G.—Daniels' single specimen so-named is the common *Bidens connata*. *C. discoidea* is not known to occur in Missouri.

1020a *Achillea Millefolium lanata* Koch—Daniels' one specimen is typical *A. Millefolium*.

1028. *Senecio tomentosus* Michx.—No specimen collected by Daniels is in the University Herbarium; but there is one so-named by him, collected by Favor, which is *S. Balsamitae*.

1036. *Centaurea Jacea* L.—All the Boone County collections so-named by Daniels are *C. vochinensis*, a species he does not mention in his *Flora*.

1042. *Taraxacum officinale* Webber—All of the specimens so-named by Daniels are the abundant species, *T. erythrospermum*, a species not mentioned in his *Flora*.

1044. *Mulgedium leucophaeum* DC.—The specimens so-named by Daniels were referred to *Lactuca villosa*, a species he does not mention in his *Flora*.

1047. *Sonchus arvensis* L.—Daniels' single collection so-named is the common *S. oleraceus*.

1048. *Lactuca virosa* L.—No specimen of this species was found in the Daniels collection, but he probably had *L. Scariola integrata* in hand when he made the determination.

1052. *Lactuca ludoviciana* (Nutt.) DC.—All of Daniels' specimens were referred to *L. Scariola*.

COURTNEY, MISSOURI

THE NATURE AND ORIGIN OF FUSAIN

C. H. CRICKMAY

Fusain, called also mineral charcoal, fossil charcoal, mother-of-coal, fusit, fusaine, and Faserkohle, has been known and variously interpreted since the early days of geology. Of the many early hypotheses concerning its nature and origin, three still have adherents.

According to the first, known as the "dry-rot" hypothesis, fusain is the product of the well known process of fungal decay known as dry-rot. Against this, it may be argued that dry-rot does not produce anything resembling fusain, and that fusain rarely if ever shows the least sign of the decay which attends dry-rot, but on the contrary is generally exquisitely preserved.

The second or "humic acid" hypothesis postulates that fusain is derived from woody debris that lay at the surface of a swamp during times of evaporation, at which times the woody matter is supposed to have become impregnated and encrusted with concentrated humic solutions. These insoluble and poisonous humic concentrates, upon drying, might have hardened and protected the wood from further decay. Under the conditions postulated, however, no product resembling fusain, that is, having among other characters a pure carbon composition, is ever formed in modern swamps or bogs. Moreover, fusain is a stratified clastic sediment commonly occurring in thin even layers; quite the reverse of the highly irregular, hummocky, residual deposit which the hypothesis would lead one to expect.

The third or "charcoal" hypothesis postulates that fusain is vegetable matter carbonized by fire. A number of objections have been made to this hypotheis but all of them seem to be readily answerable.

1. No ash beds or other evidence of burning is found with fusain; moreover the coal below it is normal and unaltered. *Answer:* the lack of evidence of burning may well be because the fires did not occur in the basin of deposition, where, certainly, they would not be expected to occur.

2. The great areal extent and regularity of successive layers is not what would be expected of an irigin by fire. *Answer:* these characters have no real bearing on the origin of the fusain; rather they indicate a particular manner of deposition.

3. The low inorganic content of fusain has been supposed to preclude all possibility of the material having been transported from land. *Answer:* charcoal is of very low specific gravity, less than 1 until it has been water-soaked, and hence would readily be separated, by the sorting action of moving water, from rock waste that might at any time be associated with it.

4. The fragility of some of the plant structures preserved as fusain are such as to preclude a fire origin. *Answer:* this argument is mainly false; no really delicate structures such as spores, pollen grains, leaf hairs, or flowers

are ever preserved as fusain. Leaves which are commonly so preserved are tough rather than fragile, and may be carbonized by heat without decrepitation.

5. The rarity of real charcoal in modern peat suggests that coal, which is assumed to have been derived from peat, ought not have any real charcoal in it. *Answer:* fusain has not yet been found in any deposit which can be shown to have originated as peat. It never has the matted or felted structure of peat. On the other hand, charcoal is not uncommon in shallow-water sediments of all kinds, including vegetable muck such as may have formed coal.

6. Fusain occurs in various states of preservation, and this lack of uniformity would not be expected if all fusain were charcoal. *Answer:* lack of uniformity is characteristic of natural charcoal which shows all degrees of carbonization; only artificial charcoal approaches uniformity.

7. Fusain actually passes into coal in places, single pieces of vegetable substances being partly fusain and partly coal. *Answer:* this condition would be expected if a stem or limb were partly burned, the charred part becoming fusain, the uncharred, becoming coal. Fires in wet swamps produce a vast quantity of partly charred fragments of vegetation.

8. The fact that fusain, in fragments and fine dust, occurs scattered through coal seems to preclude the possibility of origin by fire. *Answer:* charcoal and various forms of vegetable debris, all of which originate in forest-covered swamps, would become intimately mixed during transportation and deposition. The intimate association of fusain and coal in fragments of all sizes merely precludes the residual origin of either.

9. Certain chemical reagents produce different reactions with fusain from that which they produce with artificial charcoal, thus seeming to show that fusain and charcoal are fundamentally different substances.[1],[2] The reactions are simple ones: the reagents, benzol, potassium hydroxide, etc., extract from fusain yellow and brown colorings which are not obtainable from fresh charcoal. *Answer:* any pure substance might be expected to soak up dark coloring matters while for some millions of years in a coal bed. Moreover, samples of fusain from rocks untainted by bituminous matter, like fresh charcoal, do not respond to the chemical tests. The chemical tests therefore offer no real argument that fusain is fundamentally different from charcoal.

Having considered these questions, more positive evidence may be presented. Fusain has exactly the same chemical composition (except for absorbed impurities), micro-structure, elasticity, specific gravity (after removal of impurities), hardness, and lustre as ordinary wood charcoal. It is, therefore, reasonable to conclude that fusain is charcoal, and was produced by fire.

Petrographically, fusain is usually a conglomerate of charcoal pebbles in a matrix of powdered charcoal, or other sediment. The clastic character is most

1 Donath und Lang. Über die Untersuchungen und Wertbestimmung des Graphits. 1914.

2 Petrascheck, W. Fusain, eine fossile Holzkohle? Centralbl. f. Min. 1926.

perfectly shown by an example from a coal bed in the Cenozoic fresh-water deposits of the Mackenzie valley, a few miles south of Fort Norman, Canada. This example is unusually interesting because the rocks are peculiarly free from alteration so that the fusain is free from distortion by crushing so common in older deposits. This is good evidence that the material was pure charcoal before burial, for only so would it have sufficient elasticity to resist the effects of the compression by weight which compacted the beds and the coal. Fusain is always fragmental. Usually, the fragments are roughly rectangular, slightly curled chips such as are produced in abundance by forest fires. Some fragments are actually waterworn and rounded. Usually the deposit is a thin, even layer, finely and regularly stratified, which indicates sedimentary rather than residual origin. In places, cross-bedding shows that it was deposited from running water.

As it occurs in many thin layers within formations, fusain seems to have been produced periodically, as though by brief recurrences of a certain process. This also accords with the "charcoal" hypothesis.

Formerly, most of the known fusain has been described from Paleozoic and Mesozoic coals. For some years the writer has collected samples from other types of occurrence. In Illinois, fusain occurs quite commonly as isolated squarish chips in Pennsylvanian sandstones and composite limestones.

At Mt. Jura, California, whole segments of tree trunks of fusain have lately been found in the Upper Jurassic volcanic agglomerates. In these the fusain grades in single specimens into clear silicified wood. It would seem that only partial burning could produce such a result.

In British Columbia, near Ashcroft, fusain in squarish and rounded pieces has been found in the early Middle Jurassic marine shales and limestones. These materials show no trace of crushing but were apparently calcified before being exposed to any great compressive stress. The squarish pieces seem to be those which were buried almost as soon as they sank to the bottom; the rounded ones appear to have been water worn before being buried.

From Cenozoic deposits in Oregon, F. M. Anderson reports a treetrunk, part of which is mineralized, part carbonized. In the midst of the carbonized part was found a volcanic bomb, evidently the agent which by virtue of its heat transformed the wood into fusain.

In California, grains of fusain are found in Miocene, Pliocene, and Pleistocene sandstones. Even here, there is a great discrepancy between the size of the fusain fragments and the grain of the sediment in which they lie, the fusain fragments being the larger. This is, no doubt, because of the low specific gravity of charcoal, permitting the material to be carried by the weakest transporting agents. On account of this, fusain would not be expected in pebble beds, and indeed is rarely, if ever, found in them.

Inasmuch as fusain has been shown to occur in many formations which do not contain coal, it seems a mistake to regard it as having an origin inseparable

from that of coal. Coal and fusain are both vegetable products and hence their materials originate in the same place, but here the community of origin ends. It is to be expected that the two materials would be commonly deposited in the same place. On the other hand, many ages and many environments which produced no coal, did produce abundant fusain. In other words, coal requires very special conditions for its formation, whereas fusain requires only vegetation and an agent to set it afire.

The conclusion, therefore, that fusain represents true charcoal produced by fires seems reasonable, but the theory has further implications. In the first place, are natural fires sufficiently frequent to produce large quantities of charcoal? At present, of course, most forest fires are the work of man. However, in North America, about 10 per cent of the fires, or about 4,000 fires a year, are caused by lightning, and burn on the average 500,000 acres of land.[3] Other natural cauuses produce only a negligibly small number of fires. In any case, lightning is at present an adequate cause of fires sufficient to produce vast quantities of charcoal. There is no reason for supposing that lightning has not always been adequate.

The next question is that of transportation. Charcoal is so light that when fresh it floats. Experiments conducted by the author showed that of artificial charcoal placed upon water, most of the small pieces less than .12 cu. cm. in size sank to the bottom in a few days or weeks, although some remained floating indefinitely; slightly larger pieces, about .5 cu. cm., required one to two months to become sufficiently water-soaked to sink; and the largest pieces, 1 to 3 cu. cm., remained floating almost six months. Charcoal, therefore, possesses an important advantage over rock detritus. Much of it may float long enough to escape the wear of transportation by streams and waves. Furthermore, even if it sinks, it may be carried so readily as to be moved by agents incapable of carrying rock waste. As a result, it may be transported even into the basins of coal formation, a haven attained only by organic waste.

There is no question about preservation. Charcoal is more resistent to chemical and physical change than are many rocks. Its low hardness is its chief weakness, but as has been shown, the material may escape abrasion completely. After burial, the elasticity of the charcoal and the readiness with which it is mineralized, protect it from more profound alterations.

The deposition of charcoal involves only its becoming water-soaked and sinking to the bottom, and possibly its further transportation to the lower limit of water disturbance. It may come to rest in fresh or salt water and may be mingled with almost any sort of sediment. As it may be produced either

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3 Bulletin 111, U. S. Forest Service, Dept. of Agriculture, 1912. Forest fire statistics furnished by U. S. Forest Service. Dept. of Agriculture, U. S. A.; and Forest Service, Dept. of Interior, Canada.

See also Palmer, A. H., Monthly Weather Review, pp. 99-102, 1919; Beals, E. A., Monthly Weather Review, pp. 179-182, 1923; Show, S. B., and E. I. Kotok, Monthly Weather Review, ibid. pp. 175-180; Gisborne, H. T., Monthly Weather Review, p. 182, 1926.

irregularly or in large quantities, it may be deposited scattered through the mass of another sediment, or in thin, extensive layers repeated at intervals.

It is desirable that fusain and its meaning should become better known. The subject is not treated in textbooks of geology although in recent years it has received much attention from experts, as shown by current American and European papers. Something of the importance of forest fires in geology has lately been shown[4,5] but the general question of the rôle of fires throughout the vast span of geologic time has scarcely been touched. This broad question includes some varied problems of far-reaching importance—the geologic transformations of carbon from the quantitative point of view, the degree of conformity of ancient with modern meteorological conditions, the very doctrine of uniformitarianism itself. All these are concerned to some extent with the study of the significance of fusain.

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CANADA.

4 Blackwelder, E., Fire as an agent in rock weathering. Journ. Geol. **35**:134-140, 1927.

5 Crickmay, C. H., Geologic importance of forest fires (abstract). Geol. Soc. America, Bull. **41**: 148, 1930.

THE BURROWING ACTIVITIES OF CERTAIN CRABS AND THEIR GEOLOGIC SIGNIFICANCE

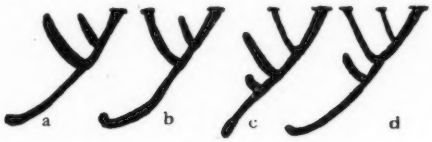
I. HAYASAKA

I.—Introduction

On the sandy and muddy beaches bordering the northwestern part of Taiwan (Formosa) there are great numbers of active crabs. Certain of these have the habit of burrowing deeply, the most common burrowers being *Ocypoda ceratophthalma* Fabricius and *Ilyoplax formosensis* Rathbun. Interested by their activities, I made plaster-of-Paris (gypsum) casts of some burrows at Tansui, a bathing place near Taihoku, the metropolis of Taiwan. Fortunately, the effort was successful, and I obtained a number of models of the burrows though many were incomplete.

Most of these closely resemble the "sandstone pipes" commonly found in certain Tertiary sandstones of Taiwan (Plate 1, Fig. 2; Plate 2, Fig. 5). Most of these are not properly pipes; they are irregularly crooked rods measuring up to a few scores of centimeters in length and one to a few centimeters in diameter. Some stand almost perpendicular to the planes of stratification, but others are variably inclined. Some of them branch.

My conclusion was that such sandstone rods would be produced if crab burrows were filled with sediment and the beach sand itself were converted into a hard sandstone. This was suggested by observations at the beach south of the city of Shintiku, southwest of Taihoku, where part of the youngest Tertiary sandstone of the island is exposed along the beach. This sandstone



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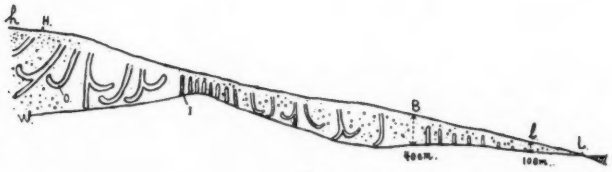

2

Fig. 1. Diagramatic representation of branched burrows made by *Ocypoda ceratophthalma*, after Takahashi. These branches are not on one plane.

Fig. 2. An ideal profile of the beach with burrows of various crabs. HB, zone of *Ocypoda ceratophthalma*. BL, zone of *Ilyoplax formosensis*. O, burrow of *Ocypoda*. I, burrow of *Ilyoplax* ,From Takahashi).

is crowded with rods, of which long and complicated examples have been removed. Before the sandstone cliff is a beach on which burrowing and other crabs are abundant.

My colleague, Mr. S. Takahashi, of the First Government Normal School of Taihoku, undertook more detailed study of these crabs, especially from the ecologic viewpoint. He succeeded in making complete casts of the burrows of *Ocypoda ceratophthalma,* as well as of *Ilyoplax formosensis.* His results have been published in Japanese papers, short but well illustrated.

Having had the privilege of examining Takahashi's materials and of working with him near Tansui, I wish to review the more important results of work on these burrows, and to indicate their geologic applications.

II.—The Burrows

The crab burrows are highly variable in size, form, and orientation, as described in my short note of 1931. Takahashi learned other interesting facts: First, the bottoms of the burrows, whether erect or inclined, reach the ground water level. Second, the burrows of *Ocypoda ceratophthalma* and *Ilyoplax formosensis* consistently differ, those of the latter species being approximately vertical and unbranched (Plate 1, Fig. 4). The complete burrows of the former, when made by large crabs, are neither vertical nor straight: they descend at an angle of about 60 degrees to the surface of the beach and on reaching the ground water level reflect at a similar angle. Commonly they return to the surface, resulting in U- or V-shaped burrows whose openings differ in diameter (Plate 2, Fig. 1). Incomplete burrows generally are the work of young, small crabs; they almost always are vertical to the surface, though incomplete large burrows are oblique to it. Y-shaped burrows sometimes are found; in these a downward branch is burrowed at the elbow of a U-shaped excavation to reach a later and lower water level. One of these was mentioned in my paper of 1931, but Takahashi gives better examples. By further addition of subordinate branches that are roughly in a plane with the primary ones, the burrows become more and more complicated (Fig. 1; Plate 1, Fig. 3).

Takahashi further remarks that the working places of *Ilyoplax* on the beach range from 10 to 40 cm. above sea level, while *Ocypoda* always burrows at a height of about 30 cm. The burrowed surface of the sandy beach is covered by a new layer of sand during each tidal advance. When it recedes, the crabs resume their activities and make openings through this new layer. In consequence of these limitations, there commonly are two distinct and almost parallel zones of burrows, each the work of one species. The effect of tide control on burrow zonation is shown by Fig. 2, taken from Takahashi.

So far as observed, the burrows of different individual crabs are never connected underground.

Sizes are variable. The smaller openings of the *Ocypoda* burrows measure 3-4 cm. in diameter, and are approximately 20 cm. deep. The length, along curvature, is 40-50 cm. The largest opening measured by Takahashi is over 65 by 75 mm. in width and length.

The burrows of small *Ilyoplax* correspond to their size, or diminish even more markedly than the smallness of the animal indicates. The largest open-

ing measured by Takahashi is 14 mm. in diameter; the length never exceeds 40 cm.

III.—Conclusions

The burrows of these crabs are of more general paleontologic interest than their comparison with Tertiary "pipe rocks" alone serves to indicate. Burrow fillings of Cretaceous age are both simple and branched; some of them show the marks of what seem to be crustacean appendages. Though it is not probable that such U-shaped burrows as *Diplocraterion* are the work of crustaceans, there are casts ("fucoids") in the Ordovician which closely resemble the Cretaceous markings mentioned. It seems probable that further studies of crustacean burrows will throw light upon other problematic fossils.

Fig. 3. Burrows of crabs on the beach near Tansui, northwest of Taihoku. The sand balls scattered on the surface were brought up from the burrows by *Ilyoplax formosensis*. The black line is 6 cm. in length.

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PLATE 1

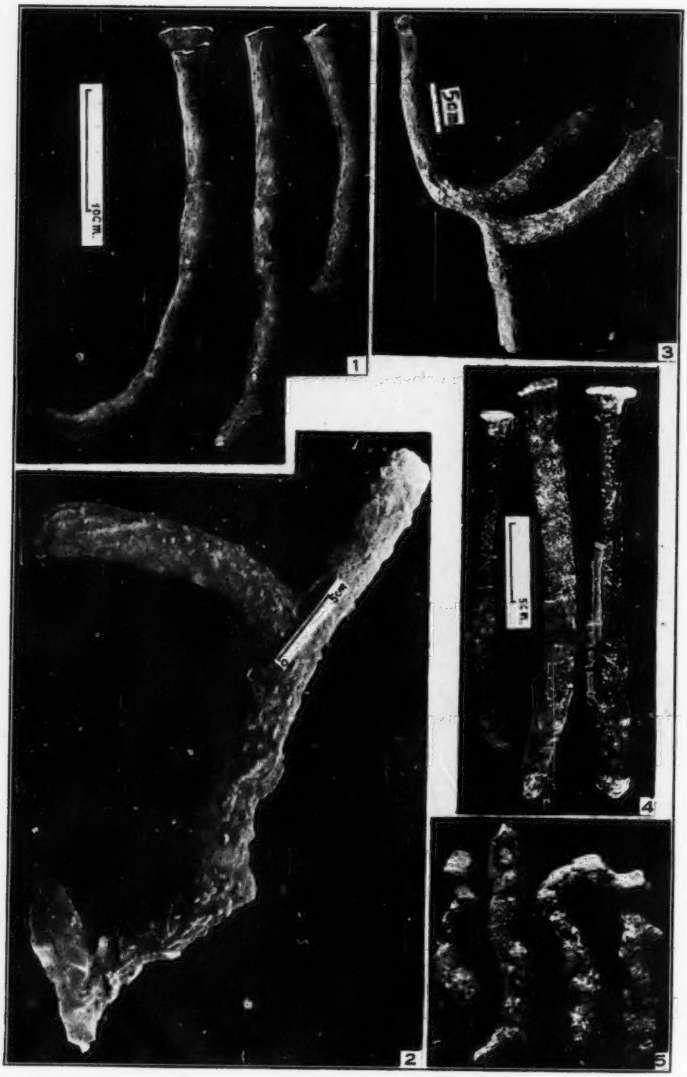
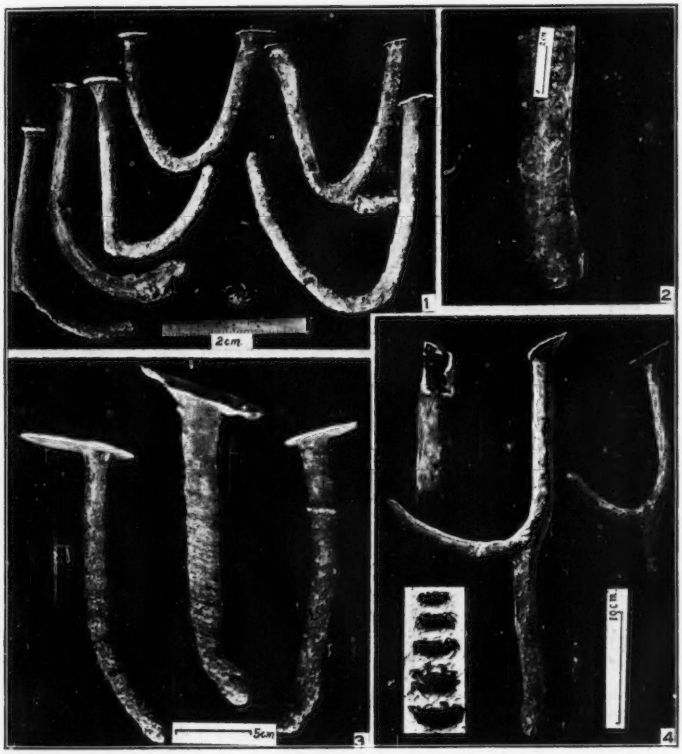


PLATE 2



FIGURES

1. Complete and incomplete U-shaped burrows of *Ocypoda*, Tansui. (Takahashi).
2. Sand rod found in hard, glauconitic sandstone of Miocene(?) age, Taityu Prefecture. The rod itself is glauconitic and contains remains of *Globigerina*, Radiolarians, etc.
3. Casts of incomplete burrows of *Ocypoda*, Tansui.
4. Y-shaped and incomplete burrows of *Ocypoda*, Tansui. (Takahashi).

(Explanation for Plate 1, on opposite page)

FIGURES

1. Incomplete casts and burrows of *Ocypoda*, Tansui. (Takahashi).
2. One of the largest burrows of *Ocypoda*, Tansui.
3. One of the complicated burrows obtained as casts. (Takahashi).
4. Casts of the burrows of *Ilyoplax formosensis* Rathbun, made by Takahashi at Tansui.
5. Four sandstone casts or rods found on the coast south of the city of Shintiku; they were weathered from the sandstone of the cliffs. About 0.3 natural size.

OTARION HALLI, A NEW NAME FOR A TRILOBITE SPECIES FROM THE HAMILTON OF NEW YORK

HARRY E. WHEELER

During a study of the genus *Phillipsia* the writer was confronted with certain nomenclatural difficulties presented by a species commonly referred to as *Cyphaspis ornata* (Hall) from the Hamilton of New York. By the solution of these difficulties it is found that the generic name *Cyphaspis* is a synonym of *Otarion*, and that the specific name *ornata* is a homonym, and must accordingly be supplanted by a new name.

The writer has not endeavored to deal with the morphology of this trilobite species, as it has been adequately described and figured by its original author.

Genus OTARION Zenker, 1833.

Genotype: *Otarion diffractum* Zenker, 1833.

The genus *Otarion* was proposed in 1833 by Zenker.[1] The type species, *Otarion diffractum*, was based upon a specimen consisting of the cephalon of a species which Barrande later described as *Cyphaspis burmeisteri*, together with the pygidium of *Calymene (?) beaumonti* Barrande, also of later date. It was the opinion of Barrande, as well as those to follow, that, since *Otarion diffractum* was based upon a composite specimen, the name is invalid, and that the respective parts of the specimen should be regarded as belonging to the later named species. Thus, the name *Cyphaspis* has been in general use until 1925, when an opinion as to its validity was handed down by the International Commission on Zoological Nomenclature.[2]

Following is the summary of the opinion:

88. OTARION DIFFRACTUM vs. CYPHASPIS BURMEISTERI.—The name of a species is not disqualified merely because the author included in his conception bodily parts of more than one species. The name of a genus based on such a species is therefore available. *Otarion diffractum* Zenker is valid. *Otarion* is to be preferred to *Cyphaspis*, and *C. burmeisteri* Barr. is a synonym of *O. diffractum*.

Extracts from the complete opinion of the Commission are as follows:

The obvious course therefore is to fix on one of the head-shields as the holotype of *Otarion diffractum* Zenker. The generic and specific names will then both hold good, and will reckon *Cyphaspis* and *C. burmeisteri* among their synonyms.

Following on this decision it is suggested that the rules should be suspended so

1 Zenker, J. C., "Beiträge zur Naturgeschichte der Urwelt. Organische Reste (Petrefacten) aus der Altenburger Braunkohlen-Formation, dem Blankenburger Quadersandstein, jenaischen bunten Sandstein und böhmischen Uebergangsgebirge." Jena, 1833.

2 "Opinions Rendered by the International Commission on Zoological Nomenclature." Smithsonian Misc. Coll. **73**(3):23, opinion 88, 1925.

as to permit the continued use of the names *Cyphaspis* and *C. burmeisteri* instead of their replacement by the hitherto unaccepted names *Otarion* and *O. diffractum*.

Cyphaspis is not a name so widely known and used as, say, *Trinucleus;* at the same time only inconvenience can be caused by changing it after nearly 80 years. The proposal may, therefore, be submitted for the vote of the Commission.

As the above proposal called solely for an opinion as to the validity of the names in question, and did not request the retention of the name *Cyphaspis*, the Commision declined to suspend the rules in this case on the grounds that "Opinions on cases not specifically submitted should be avoided on general principles." Therefore, on the basis of the decision rendered in this opinion, *Otarion* must be regarded as the valid genus, and *Cyphaspis* a synonym thereof.

Otarion halli nom. nov.

1876. *Phillipsia? (Brachymetopus?) ornata* Hall, "Illustrations of Devonian Fossils." New York Geol. Surv., pl. 21, fig. 1.

1877. *Phillipsia coronata* Miller, "The American Paleozoic Fossils," p. 221. Cincinnati. (Erroneously attributed to Hall).

1888. *Cyphaspis ornata* (Hall), "Trilobites and other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung and Catskill Groups." New York Geol. Surv., Paleon., **7**:145-146, pl. 21, fig. 1, pl. 24, fig. 21.

1889. *Cyphaspis ornata* (Hall), Miller, S. A., "North American Geology and Paleontology," p. 541. Cincinnati.

1890. *Cyphaspis ornata* (Hall), Vogdes, A. W., "A Bibliography of Paleozoic Crustacea." U. S. Geol. Surv., Bull. **63**:107.

1893. *Cyphaspis ornata* (Hall), Vogdes, A. W., "A Classed and Annotated Bibliography of the Paleozoic Crustacea." Occas. Papers Calif. Acad. Sci., pp. 89 and 296.

1910. *Cyphaspis ornata* (Hall), Grabau, A. W., and Shimer, H. W., "North American Index Fossils," **2**:302, text fig. p. 303. New York.

Not 1843. *Phillipsia ornata* Portlock, "Report on the Geology of the County of Londonderry and parts of Tyrone and Fermanaugh," p. 307, fig. 2. Dublin.

Discussion.—In 1876 James Hall[3] illustrated this species under the name of *Phillipsia? (Brachymetopus?) ornata.* This name is necessarily invalid, since it is a homonym of *Phillipsia ornata* Portlock, 1843. S. A. Miller observed this fact, and in 1877 proposed the name *Phillipsia coronata* for the species. This name was valid until 1888, when Hall removed the species from *Phillipsia,* and assigned it to *Cyphaspis,* which made Miller's name a homonym of *Cyphaspis coronata* Barrande,[4] an European species. By virtue of the change of genus, Hall believed his *ornata* to be no longer a homonym, and states that "its original specific designation may be restored, especially

3 See synonymy for citations of references not footnoted.

4 Barrande, J., "Crustacés divers et poissons de dépots Siluriens de la Boheme." Supplément au vol. 1, "Systeme Silurien du centre de la Boheme." Prague et Paris, 1872.

as *Cyphaspis coronata* is a name already used by M. Barrande." This reasoning is obviously discordant with the International Rules of Zoological Nomenclature,[5] as *Phillipsia? (Brachymetopus?) ornata* Hall is stillborn, and cannot under any circumstances be restored. Miller correctly suppressed the name, but, unfortunately, he replaced it with *Phillipsia coronata* which was destined to become another homonym.

By virtue of the above-cited opinion of the Commission on Nomenclature, *Cyphaspis* must now be regarded as a synonym of *Otarion*, and, as there exists no available specific name for the species in question, the writer proposes the name *Otarion halli* Wheeler, new name.

Holotype.—American Museum of Natural History Paleontological Collection, catalogue no. $\frac{4966}{1}$

Type locality.—"Crystalline layers of the Hamilton group, at Eighteenmile Creek, Erie County, New York."

Geologic age.—Middle Devonian.

Remarks.—This species is named in honor of its first describer, Dr. James Hall of the Geological Survey of the State of New York.

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5 "International Rules of Zoological Nomenclature." Proc. Biol. Soc. Wash., **39**, 1926, articles 35 and 36, pp. 86-87. Same, Ferris, G. F., "Principles of Systematic Entomology." Stanford Univ. Publ. Biol. Sci. **5**(3):143-144, 1928.

OVOVIVIPAROUS REPRODUCTION OF MIOCENE TURRITELLIDAE

A. H. SUTTON

I.—Introduction

A large specimen of *Turritella alumensis* Mansfield containing 48 apparently unborn young, has been found in a fossil collection made by the writer from the Choctawhatchee (Miocene) formation at Alum Bluff, Florida. This discovery gives additional information about ovoviviparous reproduction in the genus. Frank Burns[1] reported the occurrence of embryonic shells in specimens of *T. cumberlandia* Conrad and *T. indenta* Conrad, both from the Miocene beds at Plum Point, Maryland, thirty-five years ago. Since then, so far as the writer knows, nothing has appeared in print about this interesting phenomenon. At that time knowledge of reproduction among modern *Turritellidae* was not sufficient to allow comparison of fossil with living species. Because of later information about living forms, the writer believes that this ovoviviparous habit of the fossil species is of sufficient interest to warrant a short discussion. Another justification for this paper is that the subject is but little known. It is doubtful if many paleontologists have noted the paper by Burns and possibly many zoologists may be unaware of it. The writer wishes to express his thanks to Professor H. J. Van Cleave, Department of Zoology, University of Illinois, for advice while preparing the paper, and to Mr. H. L. Geis, University of Chicago, who found the little shells in the large specimen.

Knowledge of reproduction among living Turritellidae is limited. Dr. Marie V. Lebour[2], naturalist at the Marine Biological Laboratory, Plymouth, England, recently has reported on the eggs and larvae of *Turritella communis* Lamarck. According to her, *T. communis* is oviparous, the eggs requiring about a week or ten days to hatch. The newly hatched larva is colorless with a shell of one transparent whorl about 0.16 mm. across, has no special characteristics, and resembles many other grastropod veligers. Her studies of other young *T. communis* show that the adult sculpture begins on the second whorl and that the larva begins to crawl with a shell of about two and a quarter whorls, considerably smaller than our specimens. These observations would appear to offer serious arguments against our forms being embryonic, if Miocene Turritellas were as closely related to modern forms as we have believed. However, we know that notable variations in reproductive habits do occur in some groups of gastropods and it is not inconceivable that during its evolution *Turritella* may have undergone changes in its reproductive method.

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1 Burns, Frank, Viviparous Miocene Turritellidae. The Nautilus, **13**(6):68-69, October 1899.

2 Lebour, Marie V., The Eggs and Larvae of *Turritella communis* Lamarck and *Apporrhais pes-pelicani* (L.) Journ. Marine Biol. Assoc. United Kingdom **18**:499-506, Jan. 1933.

II.—Characteristics of the young shells

Burns did not describe his small shells or discuss their position in the adult. He stated only that they were about one millimeter in length and about the same in width, and assumed *a priori* that they were embryonic but gave no evidence to support his conclusion. The adult shell of *T. alumensis* consists of portions of three whorls, has a maximum diameter of 2.5 cm. and a length of about 4 cm. The shell is worn but the lowest whorl is apparently the one immediately above the apertural or last spiral whorl. The young shells were situated in the lowest whorl, a position which would be entirely suitable for unborn young, if this genus is comparable to other ovoviviparous gastropods.

The 48 individuals were rather tightly packed in the same portion of the parent shell and are all essentially of the same size and stage of development. Each tiny shell is approximately 2.5 mm. in length, and from 1.6 to 1.75 mm. in maximum width and consists of the protoconch and three spiral whorls. Spiral shells sculpture, characteristic of the species and beautifully preserved, begins on the first whorl below the protoconch. There are no signs of abrasion on either the protoconch or the remainder of the shell which clearly indicates no rolling of them either in the sediment or in the large shell which contained them. The little shells are notably larger than even the largest particles of sediment which enclosed and even filled them to a considerable extent. Careful search failed to reveal any other shells of *Turritella* or other forms comparable in size to these, either in the sediment adhering to the shells of the collection or contained in them.

III.—Hypotheses of Occurrence

There are four possible explanations of the occurrence of the small forms in the large individual: (1) they may have hatched from eggs deposited in the large shell after death of the large individual, (2) they may be the remains of young which of their own accord crawled into the large individual and there perished, (3) they might have been washed into the large shell after the death of all forms or, (4) they may represent unborn young.

Perhaps the best way to determine the embryonic nature of these small shells is to consider the hypotheses and show the inadequacy of all but the last. If these shells are the remains of individuals hatched from eggs deposited in the empty large shell, we must explain how veligers which should begin life with only one whorl to the shell could have existed here long enough to develop shells as large as these. Also it is hard to understand how shells developed under these conditions could have escaped some wear due to rolling and tumbling in the large shell while it was being worn and broken. If we assume that they crawled into the empty shell, we must explain how 48 individuals, all of the same size and stage of development, selected the same whorl of a larger shell into which to move and die. Furthermore, if forms of this size were abundant enough for such a number to congregate in one such limited space, it would appear logical to expect other similar forms in the sediment enclosing or filling other large shells.

The third possibility, that they were washed into the empty shell along with the enclosing sediment, also encounters serious difficulties. The lack of

abrasion is more of an obstacle in this case than in either of the others. Again it is asking almost too much to assume that this number of like individuals should be brought together in one such limited space by purely mechanical means. When the small shells are compared in size with the sediment in which they were imbedded, another difficulty arises. Each shell is several times the size of even the largest grain of sediment. Finally, if these small forms were abundant enough for this many to be brought together mechanically, others should be expected in the sediment, not in this shell or in this particular whorl.

There are also several features of a more positive nature which should be considered. The unabraded character suggests no movement at any time, a situation which could have been effected, it seems to the writer, only if they were embryonic and had been held almost immovable by organic matter while the fine sediment was firmly packed around them. It may appear that the size of the shells and the number of whorls constitute objections to their embryonic origin. However, in comparison to other ovoviviparous gastropods, the small shells are not out of proportion either in size or number of whorls. In some genera, which do not possess such high spires as *Turritella*, embryonic young with two and one half to three whorls have been found in adults of only six or seven whorls.[3] The discrepancy in size between our forms and those discovered by Burns is not a serious matter since it is known that the size of young at birth among living gastropods varies greatly in different species of a genus. The find corroborates and substantiates the findings of Burns thirty-five years ago, even though he reached his conclusions without reviewing other possibilities.

IV.—Conclusions

The position of the small shells in the large individual, the identity in size and stage of development of all the small forms, their unworn character, their large size in comparison to the sediment enclosing them, and their absence in the sediment from which the collection was made seem to eliminate all explanations of their occurrence except that they represent embryonic young. Evidently the mother died before birth of the young and as the body decayed, fine sediment filled the large shell preventing any wear or destruction of the small forms. If this is the true explanation, as it appears to be, we must conclude that the genus *Turritella* during its evolution from the Miocene to the present has undergone important modification of the reproductive method, the development of an oviparous from an ovoviviparous habit, or that the fossil ovoviviparous Miocene species, called *Turritella*, were not as closely related to living oviparous species of *Turritella* as formerly has been supposed.

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3 Baker, Frank C., Fresh Water Mollusca of Wisconsin. Wisc. Geol. and Nat. Hist. Survey, Bulletin **70**(1):77, 1928.

INARTICULATE BRACHIOPODS FROM THE GRASSY CREEK SHALE OF PIKE COUNTY, MISSOURI

D. K. GREGER

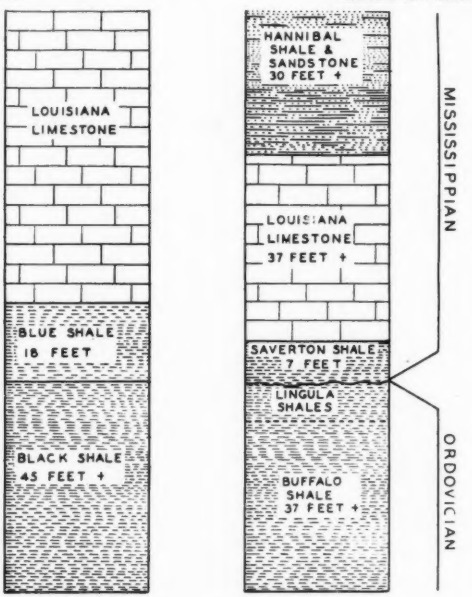
I.—Introduction

The recent discovery of *Climacograptus, Asaphus, Strophomena, Buthotrephis* and conodonts, in association with the abundant Lingulae of the Grassy Creek shale of eastern Missouri, makes it desirable that the various species of *Lingula* be described.

The black, *Lingula*-bearing shale as developed on Grassy Creek, Pike County, Missouri, has been referred to both Upper Devonian[1,2] and Lower Mississippian[3]. However, recent discoveries prove the shale to be of Ordovician age, possibly Maquoketa.

The types of *Lingula* here described and numerous supplementary examples, are in the Greger collection.

SECTIONS AT THE TYPE LOCALITY OF THE GRASSY CREEK SHALE



1 Iowa Acad. Science, **5**, 1897, p. 63.
2 Geology of Pike County. Mo. Geol. Surv., **8**, 2nd Ser., 1908.
3 Iowa Acad. Science, **19**, 1912, pp. 154-155.

II.—Description of Species

Lingula missouriensis Rowley

Plate 3, Figs. 1-3.

Lingula missouriensis Rowley, Missouri Geol. Surv. 2, 8:87, pl. 19, 19, fig. 1, 1908.

Description.—Shell, large, elongate-elliptical; sides parallel for nearly one half the length; posterio-lateral margins gently converging to form the prominent but obtusely pointed beaks. Front subtruncate; antero-lateral margins more rapidly incurved than the posterior. Surface ornamented with irregular, large and small concentric growth lines. A shallow, ill-defined median depression extends from the umbonal region to near the anterior end. Internally the suurface presents a coarse, irregularly arranged series of pits, which in the posterior region become very prominent. Average thickness of the shell over the vascular region 0.3 mm. A low median septum extends from the beak fully two thirds of the length, in the brachial valve.

Dimensions of twelve specimens give the following average: length 46 mm., breadth 22 mm.

Lingula pikensis spec. nov.

Plate 3, Figs. 4-5.

Description.—Shell small, symmetrically oval in outline, gently convex; the exterior covered with low irregular, concentric growth lines, about 16 to the space of one millimeter. Internally the shell is smooth and nacreous; a number of faint, divergent lines extend from the beak forward for nearly one-third the length. The posterior and postero-lateral margins are thickened, and form an internal ridge which stands out prominently. Measurements of a number of specimens of this abundant species give the following averages: length 5.0 mm., breadth 3.0 mm., convexity of each 0.4 mm.

Remarks.—This little species, the most abundant in the association, frequently retains traces of the original coloration, consisting of one or more concentric, black bands.

Lingula tantilla spec. nov.

Plate 3, Figs. 6-7.

Description.—This minute species is elongate elliptical, with parallel lateral margins along the middle third of the shell. The anterior margin is rounded; the posterior somewhat more angular; beaks obtusely pointed, umbones slightly inflated. The outer surface appears glabrous to the unaided eye, but under the glass, very delicate, concentric, wavy lines occupying a space of 0.001 mm. are seen to be present. Only four specimens of this species have been found; their average measurements are: length 4.5 mm., breadth 1.5 mm.

Lingula rowleyiana spec. nov.

Plate 3, Fig. 8.

Description.—In outline this species is regularly oval, with sub-acute beaks, somewhat inflated; anterior margin broadly rounded, greatest breadth forward of the median transverse line. Surface ornamented with rather distant concentric growth lines, not so delicate as in the next species described, but averaging 7 within the space of 1 millimeter. Dimensions of thirty specimens average: length 18 mm., breadth 14 mm.

Remarks.—Rowley[4] gives two figures of an unidentified *Lingula* from this

4 Missouri Geol. Survey 2, 8, pl. 17, figs. 12-13, 1908.

association, which in outline very much resembles this shell, and since the specimens are from the same locality and the same bed, they are here considered identical and the species is named for the discoverer.

Lingula yatsui spec. nov.

Plate 3, Fig. 9-10

Description.—Shell subelliptical in outline, sides sub-parallel, anterior margin truncate, with slight emargination; greatest breadth posterior to the median transverse line; beaks obtusely pointed. Surface ornamentation consists of fine, imbricating, very regularly spaced, concentric lines, 10 or 11 within the space of 1 millimeter, and by still finer, longitudinal striae. Shell substance very thin, and only infrequently preserved. Dimensions of seven specimens give the following: length 20 mm., breadth 13.5 mm.

Remarks.—Rowley's figure 11, plate 17, of the paper above referred to, was probably intended for this species. Casts of the interior of this shell show the longiutdinal lines quite plainly, and in the brachial valve is shown the impression of a low median septum which extends forwad fully one half the length of the shell. This is one of the less abundant species of the association and when the shell substance is not preserved, it is likely to be confused with *Lingula rowleyiana* described above. However, the outline of the shell, even in casts of the interior, if carefully examined, will readily distinguish the species. The specific name is for Dr. Naohide Yatsu, author of a number of papers on the recent *Lingulae* of the Japanese province.

Lingula conklini spec. nov.

Plate 3, Figs. 11-12.

Remarks.—In outline this species is oval, with the greatest diameter along the median transverse line; beaks obtuse; surface ornamented by very fine concentric lines of growth that average twelve within the space of one millimeter. Valves of this form are very thin, and with but slight convexity. This species may be distinguished from *Lingula rowleyiana*, which it most nearly resembles, by its finer growth lines, its smaller size and also by its greatest breadth being at the middle of the shell, this being a very constant feature. Measurements of ten of the best preserved specimens in the collection give the averages: length 14.5 mm., breadth 10.5 mm.

Lingula (?) insolata spec. nov.

Plate 3, Fig. 13.

Description.—This minute shell, which is referred to the genus *Lingula* with much doubt, is sub-ovate to sub-circular in outline, with obtusely pointed beaks; anterior and lateral margins symmetrically rounded, greatest convexity directly forward of the beak; surface ornamented by somewhat uneven, fimbriate, concentric growth lines, which become crowded along the front margin in the more mature specimens and form a very pronounced ridge. Dimensions of twelve specimens measured give the following: length 2.5 mm., breadth 2.0 mm.

Remarks.—The general expression of this minute form at once suggests an *Orbiculoidea* of the *O. exilis* type, but careful search through a large mass of material fails to bring to light a pedicle valve of the species.

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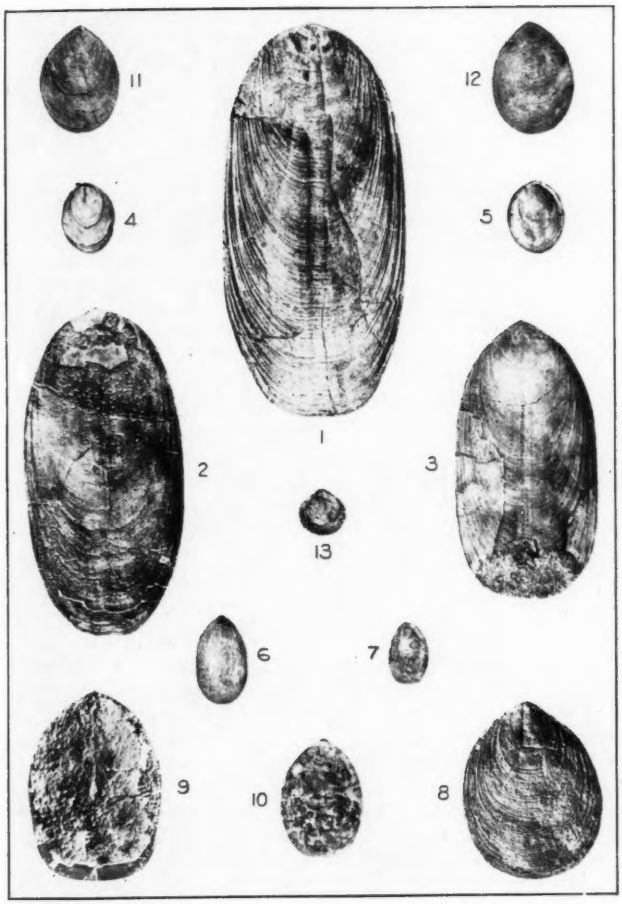
PLATE 3



(The actual measurements of each species here illustrated follow the description.)

FIGURES

1–3. *Lingula missouriensis* Rowley.
4–5. *Lingula pikensis* spec. nov.
6–7. *Lingula tantilla* spec. nov.
8. *Lingula rowleyiana* spec. nov.
9–10. *Lingula yatsui* spec. nov.
11–12. *Lingula conklini* spec. nov.
13. *Lingula? insolata* spec. nov.

ATHYRIS AND CYRTINA OF CEDAR VALLEY AGE

CARROLL LANE FENTON

I.—Introduction

Brachiopods of the Devonian Cedar Valley group in Iowa and western Illinois have received only casual published attention from Hall[1],[2] Meek and Worthen[3] and a few other workers concerned with special species or genera. Closely related and in cases identical forms were described by Cleland[4] from the Devonian of Milwaukee, though he did not distinguish Cedar Valley strata from others of apparent Hamilton age.

A few Cedar Valley species are related to others of the still younger Hackberry; some have Hamilton relatives, yet are sufficiently distinct for taxonomic recognition. Three of the latter, which have been in my hands since 1917, are here described—one to reinstate a Hall species reduced to synonymy by Schuchert, the other as a new species and subspecies.

II.—Description

Athyris vittata Hall

Figs. 1-3.

Athyris vittata Hall, 13th Ann. Rep. N. Y. State Cab. Nat. Hist., p. 89, 1860; Nat. Hist. N. Y., Pal., **4**:289, pl. 46, figs. 1-4, 1867.

Athyris fultonensis Schuchert, Bull. **87**, U. S. Geol. Surv., p. 147, 1897; *not* Swallow, Trans. St. Louis Acad. Sci., **1**:650, 1860.

Description.—Shell broadly ovate to subquadrate; length and width about equal. Dimensions of the hypotype: length of pedicle valve 13.5 mm.; length of brachial valve 11.8 mm.; width 15.4 mm.; thickness 9.4 mm.

Pedicle valve deeper than the brachial or about equal to it; beak sharp and moderately incurved. Sinus broad, subangular to rounded, generally with a pronounced lingual extension. Posterolateral regions convex; anterolateral, flattened or convex. Brachial valve convex umbonally and flattened posterolaterally. Fold high and rounded; it appears posterior to the midlength and generally is bordered by deep furrows. Both valves marked by many growth lamellae.

Remarks.—Typically, this is a Cedar Valley species, though Hall applied the name in 1867 to similar specimens from both the Onondaga and Hamilton beds of Indiana and Ohio. They, however, may be variants of the *Athyris spiriferoides* stock, homeomorphic with *A. vittata*. Since this point can be determined only by large phyletic series, no attempt at separation is made here.

Schuchert's statement that *A. vittata* Hall was a synonym of *A. fultonensis* Swallow seems to have been based on wrongly labeled material, since the latter species is small, subovate and without close resemblance to either the Ohio valley or the Iowa members of Hall's species.

1 Rep. Geol. Surv. Iowa, **1**, pt. 2, 1858.
2 Nat. Hist. New York, Pal., **4**, 1867.
3 Geol. Surv. Ill., **3**, 1868.
4 Wis. Geol. Nat. Hist. Surv., Bull. **21**, 1911.

Occurrence.—Littleton member of the Cedar Valley Group, chiefly below the chief zone of *Atrypa waterlooensis* Webster. Reported by Hall from the Onondaga and Hamilton of the Ohio valley.

Hypotype.—6693 Carnegie Museum.

Athyris vittata ovata subsp. nov.

Figs. 4-8.

Description.—Shell broadly subovate, with length and width about equal. Length of pedicle valve 13.3, 12.3 and 14.7 mm.; length of brachial valve 11.8, 11.3 and 13.4 mm.; width 13.0, 13.3 and 14.3 mm.; thickness 9.2, 10.5 and 12.3 mm. The second specimen closely approximates an early ephebic growth stage of the third.

In the pedicle valve this subspecies is distinguished by a heavier beak, convex anterolateral regions, and a sinus which is shallow and flattened, or distinguished only by the lingual extension, which is broad. The brachial valve bears a low, indistinct fold with only incipient bounding furrows prior to gerontic growth. Heaviness of the pedicle beak is the least stable of these characters.

Remarks.—While they may be of environmental origin, the distinguishing features of this subspecies are stable, and are associated with no sedimentary peculiarities. They seem, therefore, to merit recognition.

In the upper Cedar Valley (Bloody Run member of Floyd and Greene Counties, Iowa) there are diminutive forms of *Athyris* which probably are variants of this subspecies. Specimens are too poor for illustration.

Occurrence.—Littleton member of the Cedar Valley, Buffalo and Pine Creek, Muscatine County, Iowa.

Holotype.—6694; Paratypes, 6695-6696 Carnegie Museum.

Cyrtina plena spec. nov.

Figs. 9-11.

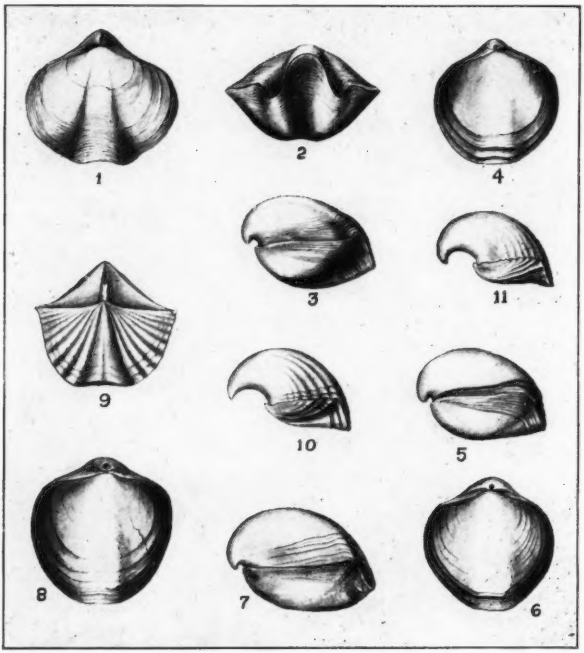
Description.—Shell small, wider than long. Dimensions of the holotype: length of pedicle valve 12.3 mm.; length of brachial valve 8.8 mm.; width 14.0 mm.; thickness 8.0 mm.

Pedicle valve strongly and almost uniformly arched, with a sharp and very prominent beak. Cardinal area strongly arched—never flat or irregularly distorted. Sinus broadly angular, bordered by high plications; extremities acute or slightly produced. Brachial valve convex umbonally, flattened to concave laterally, with a high fold bearing an indistinct medial furrow. Plications 5-7; they are strong, rounded to subangular, and separated by deep furrows.

Remarks.—The most distinctive characters of this species are its high, convex pedicle valve, sharply arched cardinal area, and freedom from distortion through attachment.

Occurrence.—Lower Littleton member, Buffalo, Iowa; corresponding beds to north and west.

Holotype.—6697; *Paratype* 6698; *Metatype* 6699 Carnegie Museum.



FIGURES

1–3. *Athyris vittata* Hall. Brachial, anterior and lateral views of the hypotype, Butler's Landing, Iowa River; Johnson County, Ia. Fig. 2 is reversed to emphasize the deep furrows bounding the fold. (6693 Carnegie Museum.)

4–8. *Athyris vittata ovata* subsp. nov.

4. Brachial view of the second measured specimen; compare with growth lines on Fig. 8. (6695 Carnegie Museum.)

5–6. Two views of a paratype with many marginal laminae, but indistinct furrows. (6696 Carnegie Museum.)

7–8. Two views of the holotype, a gerontic specimen with blunt pedicle beak. (6694 Carnegie Museum.)

All from Pine Creek, Muscatine County, Iowa.

9–11. *Cyrtina plena* spec. nov.

9–10. Two views of the holotype. (6697 Carnegie Museum.)

11. Lateral view of the paratype, with abruptly arched area. (6698 Carnegie Museum.) This and the preceding specimen are from Littleton, Iowa.

(All figures x 1.5)

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AN EXTENSION IN THE RANGE OF FOSSIL PECCARIES

C. STUART JOHNSTON

Our knowledge of fossil peccaries in the Great Plains region is extremely limited, and thus far none have been reported from Oklahoma. *Mylohyus nasutus* was apparently common in the eastern states during Pleistocene time, and the fact that we now know it to have ranged into western Oklahoma is of more than passing interest.

The oldest peccary described from North America was reported by Cook (1922) from Chadron formation nine miles north of Crawford, Nebraska. McCornack (1920) listed two undetermined species of the genus *Platygonus* from the Fossil Lake region of Oregon, and Aster Pass in California. Maxson (1930) described what appeared to be a fragment of the mandible with permanent and deciduous teeth of *Prosthennops*, the species being undetermined. This came from the lower Miocene of southern California.

East of the Mississippi fossil peccaries have been varied and abundant. A number of genera of the family *Tayassuidae* including *Mylohyus*, to which the Oklahoma specimen belongs, are described by Gidley (1921). In discussing *Mylohyus nasutus* Hay (1914) points out that a canine referred to this species was reported by Cope (1899) from a cave in eastern Pennsylvania. The type specimen of the form just mentioned was described from Indiana by Leidy (1869). One of the most widespread of the Pleistocene peccaries was *Platygonus compressus* which was figured and described in detail by Leidy (1889). Leidy (1887) compared two extinct species of the genus *Dicotyles* with *Platygonus compressus*.

In describing the Pleistocene vertebrates of Indiana Hay (1912) includes in his discussion the figures and measurements given by Leidy for the type specimen of *Mylohyus nasutus* from Gibson county. A great deal of our knowledge of this genus comes from remains discovered by Mr. Barnum Brown (1908) in the Conrad Fissure in northwestern Arizona.

The specimen to be described in this paper was found several years ago by Dr. T. C. Carter in a Pleistocene gravel bed near Alva, Oklahoma. Dr. Carter turned it over to Professor J. W. Stovall of the University of Oklahoma, and it is now in the University Museum collection, number 604. It is the only specimen of its kind that has been found in the state.

The fossil consists of the anterior portion of the skull. It is in an excellent state of preservation, and the palate is complete. The incisors, however, are missing as are also the three left premolars. The crowns of the teeth are rather badly worn, indicating that the individual was old.

The dental formula for the upper jaw is: I-2 C-1 P-3 M-3.

The measurements of the teeth are as follows:

	P2	P3	P4	M1	M2	M3
Length	9 mm.	10 mm.	12.5 mm.	14 mm.	15 mm.	18 mm.
Width	9 mm.	11 mm.	12.5 mm.	15 mm.	15 mm.	13 mm.

Longitudinal diameter of canines at the base 15 mm.
Transverse diameter of the canines at the base 11 mm.
Length of canines 36 mm.
Width of palate at the narrowest part 32 mm.
Width of jaw across sockets of the canines 54 mm.
Distance from rear of canines to front of first premolars 68 mm.
Distance from front of premaxilla to point even with anterior edge of second premolars 144 mm.
Distance from front of premaxilla to line joining hinder border of canines 63 mm.

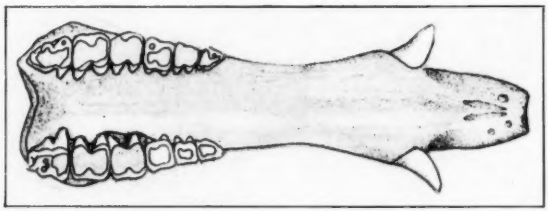

Fig. 1. Palatal view of *Mylohyus nasutus*, Oklahoma University Museum No. 604. Length 220 mm.

The alveoli of the missing incisors as shown in the drawing, Fig. 1, will illustrate sufficiently their positions and sizes. It will be noticed that the alveoli of the two right incisors appear to be conjoined, as though these two teeth were close together, while those of the left side are probably in more normal positions. The three left premolars which were not present in the fossil have been sketched in the drawing to show their relative sizes and positions. Premolars 3 and 4 are definitely molariform. Diastema is about two-thirds the length of the premolar-molar series. The palate is about one half as wide in this region as the length of the diastema. The surface of the palate is lined with parallel ridges running lengthwise, and there is a rather broad furrow in the anterior portion. A side view of the fossil is shown in Fig. 2.

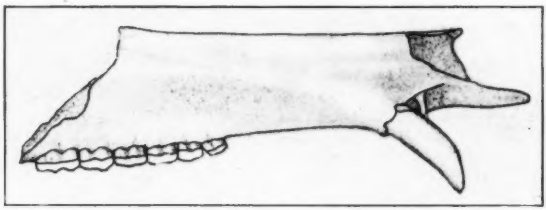

Fig. 2. Lateral view of the anterior portion of the skull of *Mylohyus nasutus*, Oklahoma University Museum No. 604. Length 220 mm.

On the basis of the characteristics and measurements given the above fossil is here identified as *Mylohyus nasutus* (Leidy). It appears to be the first of the species to be reported from the Great Plains region, and adds one more important step to our knowledge of the distribution of this group of Pleistocene mammals. We thus find *M. nasutus* ranging from eastern Pennsylvania to western Oklahoma.

It is of interest to note that in western Oklahoma, near Optima, in a sand formation of probable Lower Pliocene age, Professor J. W. Stovall found several molars belonging to an unidentified species of peccary. This find has not heretofore been reported.

Finally it may be pointed out that during the summer of 1933 the University of Oklahoma Archaeology Department while excavating an Indian village of pre-Columbian age at Optima, Oklahoma, found buried in the floor of one of the houses along with the remains of other mammals and turtles, the third and fourth metapodial bones of a small peccary of the genus *Dicotyles*. It is thus established that peccaries lived in Oklahoma in Postglacial time. According to Professor Forrest Clements this was as recent as approximately five hundred years ago. There is thus a known time range in this region for peccaries from probably Lower Pliocene to Recent.

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THE LEAST WEASEL IN MINNESOTA AND ITS FLUCTUATION IN NUMBERS

GUSTAV SWANSON AND P. O. FRYKLUND

The least weasel, *Mustela rixosa* (Bangs), is rather poorly represented in collections, and in most parts of its range has been considered rare. This is undoubtedly due at least partially to the small size of the animal, which tends to make it rarely caught in the course of ordinary fur-trapping. In recent years there have been several records from Pennsylvania, Ohio, Illinois, Indiana, and Nebraska which are referred to in papers by Dice (1928), Swenk (1926), Winecoff (1930), and Lyon (1933). These records show that the species is not as excessively rare as previous information indicated, but still much remains to be learned about the life history, and even the distribution, of the least weasel.

Although much of Minnesota offers suitable environment for the species, it has been taken in only a very few localities. Surber (1932) says that "it is probably abundant in the extreme northwestern counties of the state, particularly Roseau County, from which section ten specimens have found their way into the University collection." This is apparently the only published record of the species having been taken in Minnesota, and the specimens in question are among those which will be discussed in detail later. Dr. C. E. Johnson (1916) and Dr. Maynard S. Johnson (1930) include the least weasel in their lists of Minnesota mammals, but without mentioning any specimens actually taken. Cahn (1921) reports seeing two individuals August 14, 1919, near Cedar Lake, in Itasca County.

In addition, the species has been taken in North Dakota near the Minnesota line. The specimen in the U. S. National Museum (No. 435) reported by Baird (1857) is labelled "Pembina, Minn.", but technically it should be asigned to North Dakota, in which the town of Pembina now lies. The misunderstanding arose through the fact that before Minnesota became a state in 1858 a large part of the present Dakotas was included in the Territory of Minnesota. Another specimen taken near Minnesota was reported by Bailey (1926) as taken by Mr. H. V. Williams at Grafton, N. D. on October 24, 1913. Grafton lies in Walsh County, only 12 or 14 miles west of the Minnesota boundary. Walker (1927) reports two other specimens taken at Grafton, N. D., a male March 14, 1923, and a female December 31, 1923. All of these specimens from the northern part of Minnesota and from North Dakota are presumably *Mustela rixosa rixosa* (Bangs), the typical form, but there is evidence to show that *M. r. allegheniensis* (Rhoads) also may occur in the state, for Ward (1911) reports it from Prescott, Pierce County, Wisconsin, just across the river from Minnesota, and it has been indicated by Cory (1912) that central eastern Minnesota is probably in the belt of intergradation between the two subspecies mentioned.

While enaged in field work in the interests of the University of Minnesota Museum of Natural History in northern Minnesota during the summer

of 1932, we questioned the trappers encountered with regard to the abundance of the least weasel. Mr. Orlin Gansauge of Williams, Minnesota, reported having taken one the previous winter in Lake of the Woods County. Mr. Al Gemmeke of the Northwest Angle in the same county, said he remembered having caught such small weasels, lacking the black tip on the tail, and had thought them merely young. He said that they were rare. In December 1932, a specimen, from Williams in winter pelage, was sent by a trapper to one of the writers. Most of thetrappers, however, did not recognize the description and knew nothing of the species, so it is apparently not common. All but one of the specimens Mr. Fryklund has received were taken in Roseau County, and their distribution in time is of considerable interest. The single exception was taken Feb. 26, 1909, in Marshall County.

Mr. Fryklund has resided in Roseau County since January, 1895, and all of this time has been interested in natural history. During the period from 1895 to 1927 he had seen and handled only 7 specimens of least weasels, all of which were in the white pelage. Since then his records have been as follows. The winter of 1927-28 three specimens were brought to him, one each in November, December, and February. From November 1928 to April 1929, with about the same opportunity for receiving specimens as before, Mr. Fryklund obtained 59, distributed by months as follows: in November, 6; in December, 16; in January, 12; in February, 8; in March, 13; and in April, 4 (3 young and 1 adult). In 1929-30 the species was again abundant about Roseau and Mr. Fryklund obtained 84 specimens, distributed by months as follows: August, 1; October, 4; November, 12; December, 32; January, 25; February, 8; March, 1; and May, 1.

Since then the species has dwindled in numbers to its apparent normal level, for since the spring of 1930 only three records have been brought to Mr. Fryklund's attention. He obtained one specimen in December, 1931, and one in February, 1932, and on August 12, 1932 a female with litter of ten small young was brought to him. These records indicate a very definite increase in the abundance of least weasels in the Roseau region the two years from the autumn of 1928 to the spring of 1930. Mr. Fryklund has handled 166 least weasels in his 40 years in Roseau County, and of these, 143 were taken in the two years mentioned.

There can be no question of the actual fluctuation in numbers in this one county, because Mr. Fryklund is well known to the majority of the trappers in the vicinity. Moreover, since he pays them 50 cents each for the weasels in the flesh, and they get only 10-20 cents for them through ordinary channels, they bring to him all that they trap. Unfortunately many of them are brought in too late to be of any value as mammal skins. There is no reason to believe that this particular peak in abundance is more than a local one, although it is barely possible that as secretive an animal as the weasel might escape notice elsewhere even if it occurred in considerable numbers. The "colony" of prairie least weasels reported by Swenk (1926) in Clay County, Nebraska, seems to have exhibited a fluctuation in numbers similar to the one reported above. Swenk reports that in 1916 Mr. A. M. Brooking learned of 34 specimens of *Mustela rixosa campestris* (Jackson) taken near Inland,

throughout the year as follows: in March, 1; in April, 24; in June, 5; and in September, 4. In 1917 Mr. Brooking learned of the taking of 8 specimens in Clay County, as follows: 1 in May; a nest of 4 young, and later two females, in July; and another female on August 2. In 1918 only one specimen was taken in Clay County, and from 1919 to 1923, inclusive, none was reported. In 1924 and 1925 Mr. Brooking learned of one each year. These records are not quite as striking as the Minnesota figures, but they do indicate a high point of abundance of least weasels in Clay County, Nebraska, in 1916 and 1917. Certainly they were far more abundant in those two years than subsequently, when Mr. Brooking was also alert for records of their presence.

Hamilton (1933), in his excellent treatise on the weasels of New York, says (speaking of *Mustela noveboracensis* and *M. cicognanii):*

> As with other small mammals, weasels vary in number from year to year. Their fluctuations probably coincide with that of mice. However, in the absence of suitable food, the weasels probably move from a locality of sparse murine population to a land of plenty. It is certain that in one region of a state, reputed to have weasels at a low ebb, another region, often not far removed, will have an abundance of the animals.

He then adds that a fur-buyer in Canaan, Connecticut reported that the weasel catch during the winter of 1927-28 was twenty times as high as usual, and suggests that this may have been due, in part at least, to the "greater number of trappers, induced by the lure of extravagant prices." Hamilton also reports that Mr. J. W. Pardee found weasels excessively abundant in 1928 and 1929 in the West Canada Creek section of the Adirondacks, New York.

Another record of weasels fluctuating in numbers is a short note by Baxter and Rintoul (1928), which we will quote in full, since it is in a somewhat inaccessible source:

> Unusual numbers of Weasels—This summer and autumn, in Fife, we have noticed a quite unusual number of weasels, and were interested on going to Peeblesshire, in September, to find that they were also very abundant there and in Midlothian. We are told they are more numerous than usual, too, about Kingussie, Inverness-shire, and it would be interesting to know whether this very marked increase has taken place in other parts of Scotland and whether it extends to the Stoat.

Apparently, then, weasels exhibit decided local fluctuations in numbers which are, as yet, poorly understood. It is suggested that trappers and others who have the opportunity to do so, can accumulate many valuable data merely by keeping careful records of their catch from year to year. Most of the literature on fluctuations in numbers of animals has been concerned with those which fluctuate in more or less definite cycles. We do not imply at all that these weasel fluctuations are believed to be periodic. So few instances have been noted that it does not seem likely that they are other than sporadic, but they are nevertheless interesting. We do not venture to offer any reasons to account for them, although it does seem quite possible that they might represent concentrations of weasels in a region where food is plentiful, as suggested by Mr. Hamilton.

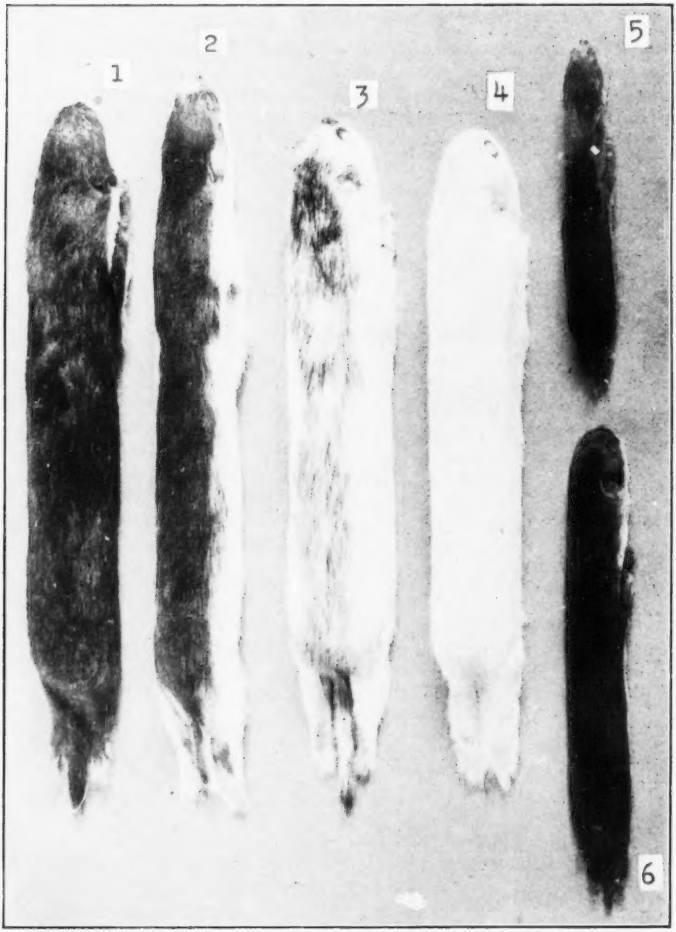
Of the 166 specimens which Mr. Fryklund has examined, 133 have been

in the white pelage, 28 in the brown, and 5 were in transitional stages between the two. These data may be of interest in greater detail. It may be said, in general, that from November through March the greater majority of the least weasels here are white, although there are a number of exceptions. Of 138 specimens which were taken during those months 125 were white, 8 were brown, and 5 were changing. The brown specimens were taken as follows: 5 in December, 1928; one January 20, 1929; one March 8, 1929; and one November 8, 1929. The individuals in transitional pelage were taken November 30, 1928; December 24, 1928; December 6, 1929; January 10, 1930; and March 30, 1930. Conversely, from April through October the majority of the weasels are brown. Twenty-one of the specimens examined were taken during this period, and only one, taken October 24, 1929, was white. Another, taken April 3, 1929, still had a small amount of white on the tail, but the remaining 19 were all in the summer pelage.

So few specimens in transitional pelage are available that the progress of the molt cannot be outlined definitely, as Mr. Hamilton has done for *Mustela cicognanii* and *M. noveboracensis*. However, from the few specimens in which we have studied it, it will be possible to indicate in general the manner of color change. Mr. Fryklund has received four specimens exhibiting a transition between summer and winter pelages. All four were more or less mottled dorsally, with brown and white hairs intermixed, as in the specimen illustrated in Figure 3. The earliest of these, taken November 30, 1928, has relatively few white hairs on the dorsum, with none at all in a small patch of brown between the ears and extending backward toward, but not quite reaching, the shoulders. The belly even in this specimen has been molted and is pure white, and the white has extended up so as to include the sides in large part. The feet and legs have much brown mixed with the white.

The latest specimen in fall transitional pelage was taken January 10, 1930. It has the mottled area covering dorsum and sides, and also shows a darker patch extending from the snout back between the ears, and behind them. This patch is also distinguishable in the December 6, 1929 specimen which is figured at No. 3. In all of these specimens the tail is evenly mixed with brown and white hairs both dorsally and ventrally. The fall molt, then, may be said to proceed about as follows. The underparts molt first, becoming pure white as contrasted with the underparts in summer pelage, when a very faint yellowish or grayish tinge may be seen. The brown sides and back are replaced by white hairs appearing very gradually, giving a mottled or "salt-and-pepper" appearance. The sides become white, the dorsum soon after. The brown color persists longest in a small patch extending from the snout backward between the ears nearly to the shoulders. Swenk's description of an adult in transitional pelage (March) together with the March 30, 1930 specimen (Fig. 2) in Mr. Fryklund's collection show rather clearly that the spring molt proceeds differently. In each specimen there is a brown band down the middle of the back, unmixed with white hairs. The line of demarcation between the white and the brown in each case is uneven, with brown and white hairs intermixed, but this intermixing of colors does not appear on the middle of the back, as in the fall molt.

Since very little is known about the breeding habit of these weasels especial note should be made of the records of young. Swenk reports four half-grown young and an adult killed April 18, 1916 by Mr. Lloyd Scherick, near Inland,



Figs. 1–6. Least Weasels from Roseau County, Minn. in Fryklund Collection. (1) No. 749. ♂. August 16, 1929. (2) No. 958. ♂. March 30, 1930. (3) No. 823. ♂. Dec. 6, 1929. (4) No. 818. ♂. Dec. 5, 1929. (5) No. 1258. ♀. August 12, 1932. One of a litter of ten. (6) No. 739. ♂. April 2, 1929. One of a litter of three.

Nebraska. Another record reported by Swenk was of a nest with four young found July 1, 1917, at Trumbull, Clay County, Nebraska. These records were for the prairie form, *M. r. campestris*. Among the specimens brought to Mr. Fryklund there have been two litters of young. April 2, 1929 three young slightly over half-grown were taken. One of these young is illustrated in Figure 6. The two specimens available for study at this time measured 121 and 112 mm. in total length, respectively. Hamilton's careful growth studies on the young of *M. cicognanii* and *M. noveboracensis* furnish our only basis for evaluating the age of these young, and even with these comparative data it is possible to estimate only very roughly. The young were probably between 6 and 8 weeks old, however, and were probably born early in February. The second litter of young in Mr. Fryklund's collection is a litter of ten, taken with the mother on August 12, 1932. The young had not yet opened their eyes, and were therefore probably less than five weeks old, undoubtedly born early in July. They varied in length from 85 to 96 mm. This litter of ten is the largest we have been able to find in a search through the literature. One of the young is illustrated in Figure 5.

Winecoff (1930) reports some interesting data on Allegheny least weasels in Pennsylvania. Here very young weasels have been killed in October, half-grown young in January, and almost full-grown young in February. He also mentions that half-grown young are seen in August more frequently. The Pennsylvania and Minnesota records show that least weasels may be born any time from July to early February in the northern states. The age of the young reported by Swenk as found July 1 is not indicated, but if they were born in May or June the breeding season in the range of the prairie least weasel may begin even earlier than any of the northern records yet known. Other species of weasels bring forth their young almost entirely in the spring.

As has been mentioned, many of the least weasels which were brought to Mr. Fryklund could not be saved as skins because of their stage of decomposition, and many of those which were saved have been scattered through sale or exchange, but the measurements of those which were still available for study have been averaged, and will be presented. Of the 107 specimens studied 97 were in the Fryklund collection and 10 in the collection of the University of Minnesota Museum of Natural History. We are indebted to Dr. Thomas S. Roberts, the director, for permission to use the latter specimens. The skull measurements were taken by Mr. Swanson from the dried skulls, and the other measurements were made by Mr. Fryklund from the fresh specimens in the flesh.

Male *Mustela rixosa rixosa* from Roseau County, Minnesota varied in total length from 165 to 217 mm., and the average of 75 specimens was 184.5 mm. It should be noted that only in very exceptional cases did they not fall within the range 170-200 mm. The tail length varied from 22 to 45 mm., and the average of 75 specimens was 31.8 mm. The hind foot length varied from 15 to 26 mm., and the average of 75 was 21.4 mm. The basilar length (of Hensel) of the skull varied from 26.9 mm. to 32.0 mm., the average of 56 specimens being 29.2 mm. The range of the zygomatic breadth was 14 to 18 mm., the average of 55 being 15.7 mm.

The females were very definitely smaller than the males in all proportions, but in some cases the measurements overlap. Total length of the females was 150 to 180 mm., with the average of 20 specimens 166.7 mm. The tail length was 18 to 33 mm., with the average of 19 specimens 27 mm. The hind foot length was 15 to 22 mm., with the average of 19 specimens 18.9 mm. The basilar length (of Hensel) of the skull was 26 to 28.5 mm., with the average of 16 specimens 27.1 mm. The zygomatic breadth varied from 13.5 to 14.5 mm., with the average of 14 specimens 13.96 mm.

It will be noted that the ratio of sexes of the specimens examined was 75 males to 20 females, or nearly 4:1. Hamilton has given several reasons to show that the sex ratio of weasels as observed in mammal collections is not a valid indication of the sex ratio in nature, and one of the reasons given obtains even more strongly in the case of the least weasel than for others, namely that since most weasels are caught in traps set for larger mammals the smaller, lighter females lack the weight necessary to spring the trap in a greater number of cases than the heavier males. There is no real reason to believe that the sex ratio at birth is not about 50:50, as would normally be expected. In the litter of 10 young there were six males and four females.

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Book Reviews

THE GRAMINEAE: A study of cereal, bamboo, and grass, by Agnes Arber. Cambridge University Press, Cambridge. xvii + 480 pp., 212 illustrations and colored frontispiece. 1934. $8.50.

Botanists have been acquainted with Mrs. Arber's work on the anatomy of the monocotyledons through a series of publications beginning nearly thirty years ago. Since 1926 these articles have dealt almost exclusively with the Gramineae, and the results of these latter studies, set against a background of significant general information drawn from the voluminous literature, are now presented in the form of a book.

It was not at all the author's aim to give an encyclopaedic account of the grass family, but, rather, to present certain features which have had greatest appeal for her. The method might well be recommended to others who feel the urge to write. The reader of this book is impressed with the feeling that every paragraph is prompted by an interest in telling something rather than by a sense of responsibility for making the book complete. On the other hand, the author's interests have been such that the book is a well-rounded, complete treatise.

The point of view is primarily morphological, but the text is generously enriched with references to the history, economic value, or other characteristics which give to the grasses their great human interest. On one page we find a translation of a Latin poem exposing the duplicity of a thrifty twelfth-century housewife, who fed her family on cheaper cereals but kept on hand a loaf of wheaten bread for the sake of proper appearances when company came. A figure copied from the palace of Sennacherib at Nineveh, showing a drove of pigs in a field of sorghum, gives a clue as to the identity of at least one variety of "corn" grown in biblical times. Again, the design on a three-thousand-year-old coin from Italy is cited as evidence that six-rowed barley has a respectable antiquity.

The treatment of the bamboos is unusually clear and complete, this marking a sharp contrast with other general works on the grasses. Although we may not entirely agree with the author in her interpretation of the phylogenetic relationship of the herbaceous and woody types, it must be admitted that there are some valid objections to the view that the former have, in general, been derived from the latter. The summary of what is known about the periodic flowering of the bamboos will be appreciated by anyone who has investigated the scattered sources.

A review of the various interpretations of the structure of the embryo and seedling shows that no explanation is entirely satisfactory. From the vascular structure of the seedlings of a number of species it is concluded that the least objectionable picture makes the scutellum and the coleoptile together the cotyledon, the mesocotyl representing the cotyledonary node and being capable of great elongation in some species.

The discussion of the grass leaf sets out anew the author's theory that there is no clear distinction between leaf and stem, but that the shoot and the root are equivalent morphological entities, the one aerial and the other subterranean.

A chapter is devoted to the question of the origin of species by hybridization, with *Zea Mays* and *Spartina Townsendi* as the outstanding examples. It is also suggested that a number of other species of grasses may have had the same origin.

The concluding chapter is a philosophical treatment of the pattern of evolution which has been carried out in the phylogeny of the Gramineae, and it is pointed out that similar themes might be discovered in other great groups of plants. This view of a scientific problem is particularly irritating to some mechanists, but to anyone who is familiar with the parallelism exhibited in the tribes of grasses it constitutes one of the most fascinating parts of the book.

The number of figures (212) gives no idea of the richness of illustration, for most

of the figures consist of many parts, a large number of them being full-page composite groups In many instances these groups, with their profuse labels, are at first confusing; but they are neat, clear, and complete, and the information that they intend to convey is there. The difficulty, if any, encountered in reading them is really one of the problem itself rather than one of technique.

Little short of a miracle could guarantee that a book of this scope would be absolutely free of errors. A few have been found.

Arundinaria tecta (Walt.) Muhl. is not the only member of the Bambuseae found wild in North America, as stated on page 59. There are at least two other species of Arundinaria, three of Arthrostylidium, and seven or eight of Chusquea in Mexico and Central American countries.

I find no authority for the use of the word "break" (instead of brake) on page 89, line 9.

From the statement on page 152 one who is not familiar with the grasses might infer than monandrous or diandrous flowers were much less common than they are. This impression would be dispelled by reading the remainder of the book, but the facts should have been made more clear at this point.

On page 199 the spikelet of *Holcus lanatus* L. is described as two-flowered with the lower flower male and the upper hermaphrodite. Figure 99, B3, page 201, shows the lower perfect and the upper staminate. The figure is correct.

The statement that shortening of the day retards flowering in the Gramineae (p. 214) is not true of Euchlaena, Zea Coix, Polytoca, or Sclerachne. The writer has for years shortened the day for these plants as a method of bringing them to maturity within the growing season in Indiana. It is strongly suspected that many tropical species of the Panicoideae would respond in the same way.

Figure 183, A, shows, between the functional and rudimentary flowers of the spikelet of maize, a small structure which is explained in the label and in the text (p. 357) as the palea of the upper flower fused with the rachilla, and bearing a third lemma. Having sectioned some thousands of spikelets of maize and its relatives I believe that either this spikelet involves a rare anomaly or the interpretation is incorrect. Although some of the German investigators have reported finding the true end of the rachilla in the spikelets of practically all the grasses which they have examined, I know of no conclusive indication that the rachilla is prolonged beyond the second palea in any member of the Panicoideae. This is a point of some significance, because in this entire sub-family the upper flower seems to precede the lower in development, while the reverse order is followed in all members of the Pooideae which have more than one flower in the spikelet. Even in those anomalous varieties of maize in which the spikelet primordium grows out into a tiny ear or bulbil it is a question as to whether it is the end of the rachilla or the flower primordium which makes the extra growth.

The manufacture of the volume is in keeping with the high standards of its publisher. We seldom find a specimen of printing that is more nearly perfect.

The index is detailed, and its contents significant and accurate. The bibliography consists of more than 600 titles, every one of which seems to be cited in one or more places in the text.

To those interested in the morphology of monocotyledonous plants, or in the grass family in any way, the book will be indispensable.—PAUL WEATHERWAX.